

Research



Cite this article: Graf N, Bucher R, Schäfer RB, Entling MH. 2017 Contrasting effects of aquatic subsidies on a terrestrial trophic cascade. *Biol. Lett.* **13**: 20170129. <http://dx.doi.org/10.1098/rsbl.2017.0129>

Received: 1 March 2017

Accepted: 2 May 2017

Subject Areas:

ecology, environmental science

Keywords:

aquatic-terrestrial linkages, indirect effects, prey choice, spiders, aquatic subsidy, trophic cascades

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Contrasting effects of aquatic subsidies on a terrestrial trophic cascade

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Subsidies from adjacent ecosystems can alter recipient food webs and ecosystem functions, such as herbivory. Emerging aquatic insects from streams can be an important prey in the riparian zone. Such aquatic subsidies can enhance predator abundances or cause predators to switch prey, depending on the herbivores. This can lead to an increase or decrease of *in situ* herbivores and herbivory. We examined the effects of aquatic subsidies on a simplified terrestrial food web consisting of two types of herbivores, plants and predators (spiders). In our six-week experiment, we focused on the prey choice of the spiders by excluding predator immigration and reproduction. In accordance with predator switching, survival of leafhoppers increased in the presence of aquatic subsidies. By contrast, the presence of aquatic subsidies indirectly reduced weevils and herbivory. Our study shows that effects of aquatic subsidies on terrestrial predators can propagate through the food web in contrasting ways. Thereby, the outcome of the trophic cascade is determined by the prey choice of predators.

1. Introduction

Consumers can benefit from the dispersal of organisms across ecosystem boundaries, which can in turn affect food webs [1]. Such subsidies can cause different responses in the recipient food web. First, an increase of predator abundance can affect the *in situ* prey (i.e. apparent competition) [2]. Second, a switch from *in situ* to subsidy prey can reduce predation pressure on the *in situ* prey [3]. Streams and their riparian zones represent ecosystems that are linked via fluxes of material and organisms [4]. Aquatic subsidies like aquatic insects typically complete their life cycle in the terrestrial ecosystem [5] and can be an important prey for terrestrial predators such as riparian spiders [6]. Consequently, the abundance of terrestrial spiders can be enhanced along streams, reducing terrestrial insects and herbivory [7]. In the field, this apparent competition between aquatic insects and terrestrial herbivores is mediated by predator numbers, but it remains unknown if differences in predator density in riparian areas are a result of aquatic subsidies or differences in habitat conditions [8]. By contrast, indirect positive effects of aquatic subsidies on terrestrial herbivores were observed, presumably caused by a switch of a riparian predator from leafhoppers to the subsidies [9]. Such indirect positive effects of aquatic subsidies on terrestrial herbivores can dominate in riparian food webs [9,10]. However, indirect effects of such subsidies depend on differences in the quality and mobility of prey species [11]. Studies on the role of aquatic subsidies for plants [7,12] and for trophic cascades including more than one prey type in an experiment [9] are scarce. We examined how aquatic subsidies affect a terrestrial model food web consisting of two types of herbivores with differing predator avoidance strategies, plus plants and spiders. We focus on short-term effects by keeping predator numbers constant, thus excluding predator immigration and reproduction.

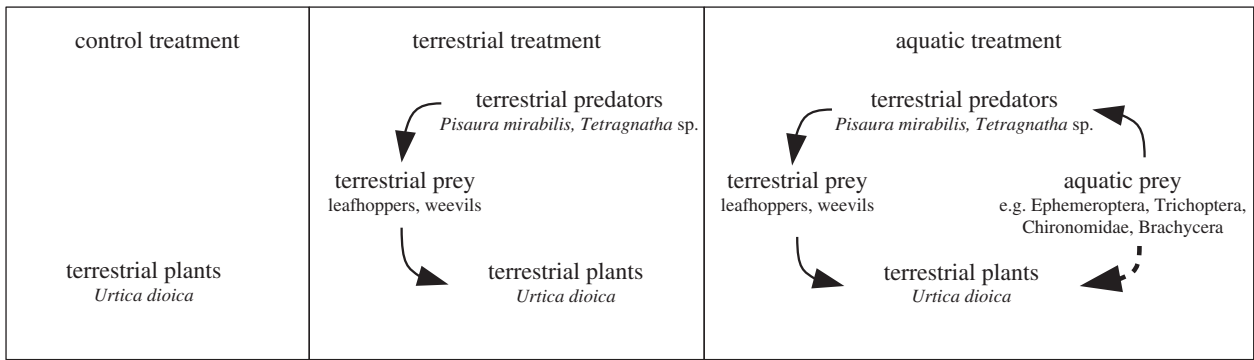


Figure 1. Design of the three treatments (control: only plants; terrestrial: terrestrial plants, prey and predators; aquatic: terrestrial treatment including aquatic subsidies). Solid lines indicate direct effects between organisms and dashed lines potential indirect effects of aquatic subsidies.

We hypothesized: (H1) different survival of the two terrestrial herbivores in the presence of aquatic subsidy, and (H2) increased herbivory in the presence of aquatic subsidy due to predator switching.

2. Material and methods

(a) Study species

We used species that are common on riparian nettle stands of the study region in realistic field densities. Spiders, *Tetragnatha* sp. and *Pisaura mirabilis*, were collected from late April until early May. *Tetragnatha* was chosen because it is common in riparian areas and feeds on aquatic subsidies [13] and *Pisaura* because it appears in high numbers on nettle plants and uses them as a hunting ground [14]. *Tetragnatha* relies on orb webs for prey capture, while *Pisaura* is a non-web-building sit-and-wait predator that can also patrol vegetation for prey [15]. Leafhoppers and weevils (*Phyllobius* sp.) were used as terrestrial herbivores and are common on riparian nettle stands. While leafhoppers feed on plant sap, weevils feed on the leaf lamina and are thus responsible for the leaf damage in previous field experiments [14]. Leafhoppers avoid predation mostly through their effective sensing of approaching predators in combination with escape movements. Weevils, rather, rely on their mechanical defence plus thanatosis to avoid predation [16]. Nettles, *Urtica dioica*, were used as a model plant to determine herbivory, because they are widely distributed along streams and offer a habitat for a high diversity of arthropods [17]. Nettles were collected four weeks before introducing them into the mesocosms from the riparian zone of a stream and were planted in fertilized soil (nitrogen 230 mg l⁻¹) in 6 × 6 × 9 cm pots. The plants were vacuumed for 5 s to remove herbivores before the experiment; slugs and snails were removed by hand.

(b) Experimental design

We conducted a six-week mesocosm experiment beside a stream in the research facility Eußerthal (49°15'17.86" N 7°57'41.69" E) in southwest Germany. The experiment consisted of three treatments: control (plants only, six replicates), terrestrial food web (plants, terrestrial herbivores and spiders, 13 replicates) and terrestrial food web with aquatic subsidies (as previous plus aquatic subsidies, 13 replicates) (figure 1). Organisms were introduced in 25 × 25 × 90 cm mesocosms (aerarium by Matthäus Hahn e.K., Altdorf, Germany). One specimen of *Tetragnatha* and two female and one male *Pisaura* per mesocosm were introduced in the food web treatments. If either *Tetragnatha* or *Pisaura* disappeared completely from a mesocosm, this was compensated by adding a new individual of the respective species. Five leafhoppers and two or three individuals of weevils were introduced

fortnightly and weekly, respectively. To quantify herbivory, three leaves per plant in each mesocosm were marked with a coloured string at study initiation. The marked leaves were photographed twice per week. Herbivory was quantified by subtracting the areas of individual leaves from the first and last picture using the software ImageJ v. 1.48v [18]. Owing to leaf fall, one additional leaf was marked in the third and in the fifth week. The length of each nettle shoot was measured on the first and last day of the experiment. After the experiment, dry weight of nettles was determined after drying for 24 h at 60°C. Aquatic insects were collected from the stream using emergence traps with a basal area of 0.25 m² each; thus the input mimicked the quantitative and temporal pattern of field emergence (see [19]). The living insects from one randomly chosen emergence trap were transferred to each mesocosm twice a week. At the end of the experiment, organisms were collected by vacuuming the mesocosms and plants for at least 5 s with a leaf blower (modified STIHL SH86 blower; Stihl, Waiblingen, Germany) to quantify the number of survived individuals.

(c) Data analysis

Treatment effects on spider survival and size were tested with a generalized linear model (GLM) with Poisson distribution, followed by an ANOVA with a χ^2 -test. To test the effects on *Pisaura* biomass a linear model was used. Effects of aquatic subsidies on herbivores were tested with a GLM with Poisson distribution, followed by an ANOVA with a χ^2 -test. To test whether the two herbivores respond differently to the treatments we conducted a GLM with binomial error distribution. To evaluate the effects of aquatic subsidies on herbivory, we calculated the weighted mean of consumed leaf area per plant and day, given the different time spans of leaf observation. A generalized linear mixed model (GLMM) with gamma distribution, log link and the individual plant as random effect was used to account for between-plant variation using penalized quasi-likelihood (PQL) [20]. Again GLMMs, but combined with a PQL and a Tukey test, were performed to test for significant differences of the plant metrics between the treatments [21]. Statistics and graphics were done in R v. 3.3.1 [22].

3. Results

Although we observed *Pisaura* and *Tetragnatha* consuming aquatic subsidies, no effect of the treatment on the survival (*Pisaura*: $\chi^2_{24} = 0$, $p = 1$; *Tetragnatha*: $\chi^2_{24} = 0.7$, $p = 0.405$), biomass ($F_{22} = 0$, $p = 0.901$) or size ($\chi^2_{24} = 0$, $p = 0.922$) of the predators was detected. The indirect effect of aquatic subsidies differed significantly between the two types of

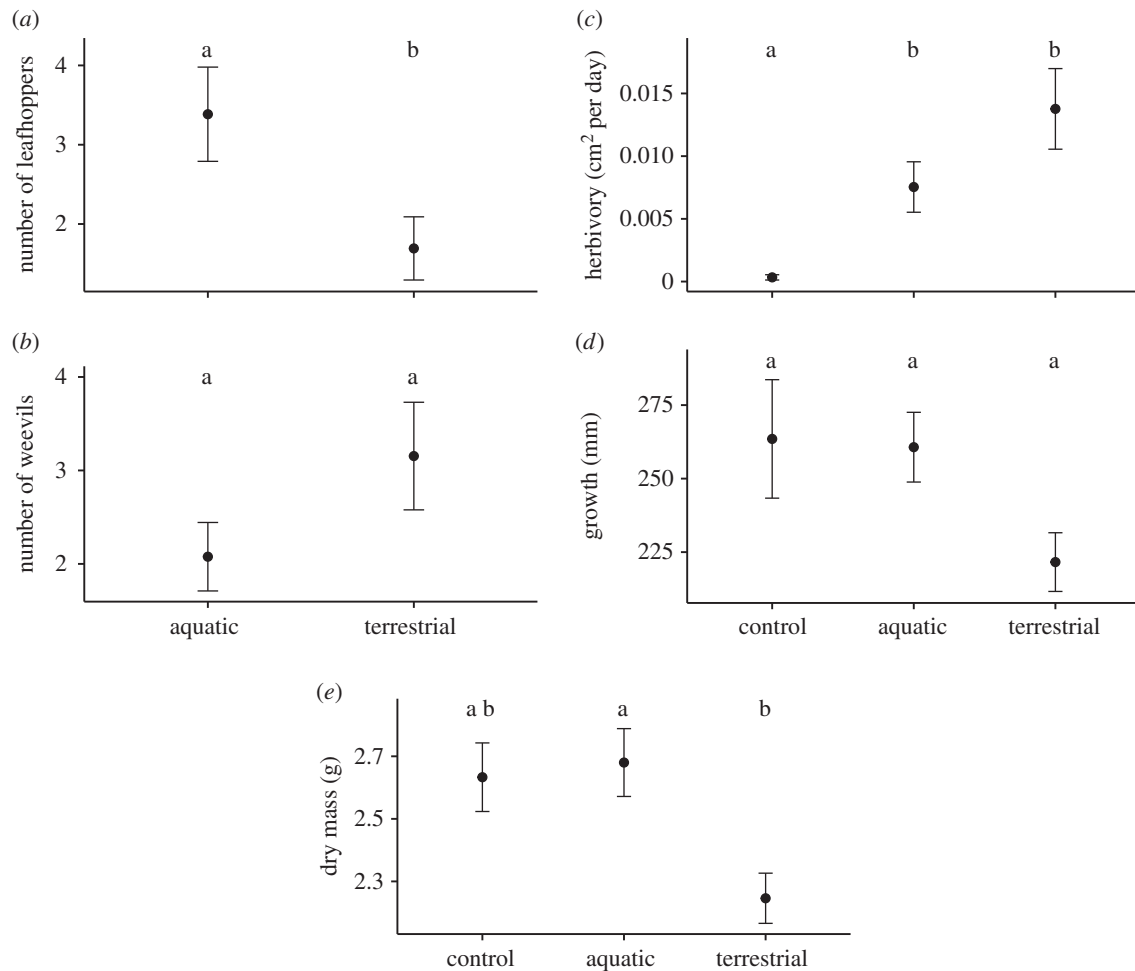


Figure 2. Effects of aquatic subsidies on (a) number of leafhoppers, (b) number of weevils, (c) herbivory (cm^2 per day), (d) plant growth (mm), (e) plant dry mass (g). Control: only plants; terrestrial: control + herbivores + spiders; aquatic: terrestrial + aquatic subsidies. Letters indicate means that are significantly different ($p < 0.05$). Data are presented as mean (filled circle) \pm s.e.

herbivores ($t_{24} = 2.9$, $p = 0.009$). The addition of aquatic subsidies caused an increased survival of leafhoppers (figure 2a; $\chi^2_{24} = 7.5$, $p = 0.006$), and there was a non-significant trend for weevil numbers to decrease in the presence of aquatic subsidies (figure 2b; $\chi^2_{24} = 2.9$, $p = 0.088$), in accordance with leaf area loss. Herbivory was reduced by 55% in the aquatic compared with the terrestrial food web treatment (figure 2c; $z_{28,128} = 2.2$, $p = 0.064$). Plant dry mass of the aquatic treatment was 1.19 times higher than without the addition of aquatic subsidies (figure 2e; $z_{28,126} = -2.3$, $p = 0.046$), with a similar trend for growth (figure 2d; $z_{28,126} = -2.2$, $p = 0.063$).

4. Discussion

As hypothesized, the effect of aquatic subsidies on weevils was different from that on leafhoppers. Leafhopper survival increased in the presence of aquatic subsidies. Similarly, a previous experiment found enhanced leafhopper survival in the presence of aquatic subsidies in an arctic ecosystem with wolf spiders as predators [9]. Opposite to leafhoppers, predation of weevils increased in the presence of aquatic subsidies. Weevils use thanatosis and mechanical defence [16] to avoid predation. When the mobility of hungry predators is enhanced in the presence of aquatic subsidies, this could lead to higher encounter rates and predation on the

relatively stationary weevils. In addition, spiders might invest relatively more time and energy for capturing highly active and relatively small-bodied prey such as chironomids. Under this situation, spiders might prefer the larger and higher-quality weevils to the plant sap feeding leafhoppers. As an alternative explanation for the decrease of weevils under aquatic subsidies, a higher leafhopper herbivory in this treatment could have induced plant defence compounds that may have caused higher movement in weevils, enhancing their encounter rate with and mortality due to *Pisaura* [23,24]. Future research should test these hypotheses to uncover the underlying mechanisms.

The outcome of the trophic cascade of aquatic subsidy on the terrestrial food web contrasted with our hypothesis. Rather than reducing plant dry mass through the release of terrestrial herbivores from predation, plant dry mass increased along with a non-significant reduction in herbivory and higher growth in the treatment receiving aquatic subsidies. This can be explained by the reduction of leaf chewing weevils in the presence of aquatic subsidies. Plant performance was more strongly affected by the reduction of the main herbivore (weevils) than by enhanced plant sucking leafhopper densities.

Even leafhopper densities can respond to aquatic subsidies in contrasting ways. The enhancement of leafhoppers by aquatic subsidies in our study and in a previous experiment [9] contrasts with reduced leafhopper densities on

nettle plants next to a river in a field survey [7]. The difference is probably due to predator accumulation in these prey-rich areas, which was excluded from both experimental studies. Accordingly, short-term release of leafhoppers from predation in the presence of alternative prey would turn into enhanced leafhopper predation after predator densities have responded to the availability of aquatic food. Thus, indirect effects of aquatic subsidies on terrestrial food webs represent a case of transient dynamics caused by resource pulses [25], whereby short-term release of (at least some) *in situ* prey from predation contrasts with a long-term increase in predation pressure. Our observation that even short-term effects of subsidies affect *in situ* prey in contrasting ways further highlights the complexity of effects of aquatic subsidies on riparian food webs.

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