

# Direct and indirect bottom-up and top-down forces shape the abundance of the orb-web spider *Argiope bruennichi*

Odile T. Bruggisser<sup>a</sup>, Nadine Sandau<sup>a</sup>, Gilles Blandenier<sup>a,b</sup>, Yvonne Fabian<sup>a</sup>, Patrik Kehrli<sup>c</sup>,

Alex Aebi<sup>d</sup>, Russell E. Naisbit<sup>a</sup>, Louis-Félix Bersier<sup>a</sup>

<sup>a</sup>University of Fribourg, Unit of Ecology & Evolution, ch. du Musée 10, CH-1700 Fribourg, Switzerland

<sup>b</sup>Centre Suisse de Cartographie de la Faune (CSCF), Passage Max-Meuron 6, CH-2000 Neuchâtel, Switzerland

<sup>c</sup>Station de Recherche Agroscope Changins-Wädenswil ACW, Nyon, Switzerland

<sup>d</sup>Laboratory of Soil Biology, University of Neuchâtel, Emile-Argand 11, CH-2000 Neuchâtel, Switzerland

---

## Abstract

Species abundance in local communities is determined by bottom-up and top-down processes, which can act directly and indirectly on the focal species. Studies examining these effects simultaneously are rare. Here we explore the direct top-down and direct and indirect bottom-up forces regulating the abundance and predation success of an intermediate predator, the web-building spider *Argiope bruennichi* (Araneae: Araneidae). We manipulated plant diversity (2, 6, 12 or 20 sown species) in 9 wildflower strips in a region of intensive farmland. To identify the major factors regulating the distribution and abundance of *A. bruennichi*, we quantified three characteristics of vegetation (species diversity, composition and vegetation structure) as well as the spider's prey community and natural enemies. The distribution and abundance of *A. bruennichi* was regulated by combined bottom-up and top-down processes as well as by direct and indirect interactions between trophic levels. Four main factors were identified: (1) the strong direct effect of vegetation structure, (2) the positive effect of plant species diversity, which affected spider abundance directly and indirectly through increased densities and size of flower-visiting prey species, (3) the positive or negative direct effects of different plant species, and (4) the strongly negative direct effect of predacious hornets. The advantage of taking a global approach to understand the regulation of species abundance is highlighted first by the quantification of the relative importance of factors, with a surprisingly strong effect of hornet predators, and second by the discovery of a direct effect of plant diversity, which raises intriguing questions about habitat selection by this spider.

## Zusammenfassung

Die Abundanz einer Art in einer lokalen Gemeinschaft wird durch bottom-up- und top-down-Prozesse bestimmt, die direkt oder indirekt auf die betrachtete Art wirken können. Studien, die beide Effekte gleichzeitig untersuchen, sind selten. Hier untersuchen wir die direkten top-down- und die direkten und indirekten bottom-up-Effekte, die die Abundanz und den Fangerfolg der Radnetzspinne *Argiope bruennichi* (Araneae: Araneidae) bestimmen. Wir manipulierten die Pflanzendiversität (2, 6, 12 bzw. 20 ausgesäte Arten) in neun Blühstreifen in einer Region mit intensiver landwirtschaftlicher Nutzung. Um die wichtigsten Faktoren, die die Verteilung und Abundanz von *A. bruennichi* bestimmten, zu identifizieren, quantifizierten wir drei Eigenschaften der Vegetation (Artendiversität, Zusammensetzung und Struktur der Vegetation) sowie das Beutespektrum der Spinne und

ihre natürlichen Feinde. Die Verteilung und Abundanz von *A. bruennichi* wurde von kombinierten bottom-up- und top-down-Prozessen sowie durch direkte und indirekte Interaktionen zwischen den trophischen Ebenen gesteuert. Vier Hauptfaktoren wurden identifiziert: (1) der starke direkte Einfluss der Vegetationsstruktur, (2) der positive Effekt der Pflanzendiversität, der die Abundanz der Spinnen direkt und indirekt durch erhöhte Dichte und Größe der blütenbesuchenden Arten beeinflusste, (3) der positive bzw. negative Effekt von bestimmten Pflanzenarten und (4) der stark negative Effekt der räuberischen Hornissen. Der Vorteil eines globalen Ansatzes, um die Regulation der Abundanz dieser Art zu verstehen, wird herausgestellt durch die Quantifizierung der relativen Bedeutung der Faktoren (mit einem überraschend starken Effekt der Hornissen) sowie durch die Entdeckung eines direkten Effekts der Pflanzendiversität, wodurch sich interessante Fragen zur Habitatwahl dieser Spinnenart ergeben.

## Introduction

Trophic regulation by either resources (bottom-up) or natural enemies (top-down) is a prime determinant of community structure (Hunter and Price 1992). Species abundance in local communities is the result of a combination of bottom-up and top-down forces, however studies considering both effects simultaneously are much rarer than those focussing on a single direction (Walker and Jones 2001). For example, spider abundance is often seen as bottom-up regulated by prey availability (e.g., Greenstone 1984; Halaj, Ross, & Moldenke 1998; Harwood, Sunderland, & Symondson 2001), or in the specific case of web-building spiders by the physical structure of the vegetation (Halaj et al. 1998; McNett and Rypstra 2000; Pearson 2009; Rypstra and Carter 1995; Sanders, Nickel, Grutzner, & Platner 2008; Topping and Lövei 1997). Spiders are also preyed upon by a variety of natural enemies (Foelix 2010), but surprisingly the contribution of top-down processes to their regulation has rarely been assessed (e.g., Askenmo, von Broemssen, Eckman, & Jansson 1977; Spiller and Schoener 1994).

The structure of the vegetation directly affects the distribution and abundance of web spiders. Other characteristics of plant communities, such as species diversity or plant composition, may also play a role but have been less well investigated. These characteristics may affect spider communities directly or indirectly via an influence on the prey community. Indirect interactions are likely, since it is well known that plant species diversity (Siemann, Tilman, Haarstad, & Ritchie 1998) and plant composition (Schaffers, Raemakers, Sykora, & Ter Braak 2008) affect insects, the main prey of spiders.

In this study, we investigated bottom-up and top-down forces regulating the abundance and predation success of an intermediate predator, the orb-web spider *Argiope bruennichi* (Scopoli). This species is a generalist predator that mostly captures diurnal insects, and which can play an important role in natural pest control (Nyffeler and Benz 1981; Rypstra and Carter 1995). It is very common in southern Europe and has been expanding northward in recent decades (Kumschick, Fronzek, Entling, & Nentwig 2011). Most studies on *A. bruennichi* examined its behaviour (e.g., Moon,

2012; Walter, Westphal, Bliss, & Moritz 2011; Welke & Schneider 2010; Zimmer, Welke, & Schneider 2012) or its dietary biology (e.g., Ludy, 2007; Malt 1994; Nyffeler & Benz 1978; Prokop & Gryglakova 2005). However, few –if any – have considered how it is embedded in ecological networks and how its abundance is affected by biotic interactions. We studied *A. bruennichi* in wildflower strips within an agricultural landscape in Switzerland. We manipulated plant diversity and plant composition in these semi-natural habitats and identified the natural prey and predator community of *A. bruennichi* in order to determine the major bottom-up and top-down forces shaping this system. We evaluated the presence of natural enemies, the abundance of potential prey, and three characteristics of the vegetation (i.e., species diversity, plant composition and vegetation structure) to answer the following questions: (1) Does vegetation affect the predation success of *A. bruennichi*? (2) Is the abundance of *A. bruennichi* mediated by bottom-up and/or top-down processes? (3) Do these bottom-up and top-down processes act directly and/or indirectly? (4) What is the relative importance of these interactions?

## Materials and methods

### Study site and experimental design

To investigate interactions in the food web centred on *A. bruennichi*, experimental wildflower strips were used, established for the purpose of a larger research project to better understand the structure and functioning of metacommunities (see Appendix A). The 12 wildflower strips, each of 648 m<sup>2</sup> (9 m × 72 m or 6 m × 108 m), were planted in spring 2007 within an intensively managed agricultural landscape in the lowlands of western Switzerland. Each wildflower strip was subdivided into three blocks, each of area 216 m<sup>2</sup>. The blocks consisted of the same repetition of four plant diversity levels (2, 6, 12, 20 sown species) arranged in plots of 6 by 9 m (Appendix A, Fig. A1). Plant species composition in each plant diversity plot was chosen by constrained random draw from a pool of 20 plant species (Appendix A, Table A1), and the order of the plots was randomly chosen in each

wildflower strip. The experimental plots were not weeded, with the exception of the two agricultural weeds *Cirsium arvense* and *Rumex obtusifolius*. In addition, *Chenopodium album* and *Amaranthus retroflexus* were removed in the first year in order to prevent light competition during germination.

## Sampling of fauna and flora

*A. bruennichi*. Males are much smaller and of shorter lifetime than females and rarely build webs when adult (Merrett 1968), so only adult females were considered in this study. Webs were recorded in nine of the twelve wildflower strips in 2008 and 2009 from late July to early August, in a randomly chosen order. Sampling took place on sunny and calm days, from 10 am until 6 pm, along a 6 m transect to a width of 50 cm on each side, ignoring those webs built directly along the central 30 cm wide path. For each plot, the presence/absence and the abundance of *A. bruennichi* (measured as the number of occupied webs) was recorded. The identity of support plants (only in 2009) as well as the number and identity of wrapped prey were recorded for each web. All prey species were collected from the webs for subsequent determination to the order level. If the prey was intact, its volume was estimated from body width and length, using the equation for a prolate spheroid (Hofer, Bauer, & Bersier 2003). Predation success was described at the plot level by the trapping efficiency, calculated as the proportion of webs containing prey, and at the web level by the volume of the largest prey.

*Vegetation*. Sampling of the vegetation in the 12 strips took place in 2008 and 2009 between July and October. In all plots the total number of plant species was determined and their individual percentage cover estimated visually. The total number of plant species in the plots ranged from 6 to 42 in 2008, and from 7 to 35 in 2009. Three characteristics of the vegetation were used in the analyses: species diversity, composition and vegetation structure. Species diversity was expressed as the effective number of species (Jost 2006). This value represents species richness corrected by relative abundance (here cover). Note that the effective number of plant species was strongly correlated with the number of species sown in a plot (Spearman  $r = 0.49$ ,  $P \leq 0.001$ ). The effect of plant composition was taken into account in two ways. First, as the log transformed cover of two species disproportionately chosen for web construction (*Malva moschata* and *Malva sylvestris* pooled) and one disproportionately avoided species (*Dipsacus fullonum*) (Appendix A, Fig. A2). Second, for the path analysis (see below), as the score of each plot on the first axis of an ordination based on global plant species composition (Fabian et al. 2012; Kahmen et al. 2005). We used a Correspondence Analysis (CA) on log-transformed plant covers, using the package *vegan* (Oksanen et al. 2010) in R (R Development Core Team 2009). The variance explained by the first CA axis was low (8%), which reflects the heterogeneity in species

composition, but is also a consequence of the large number of plots ( $n = 288$  for this analysis). Vegetation structure was characterized by the average vegetation height and by above-ground vegetation biomass. The latter was estimated in 2008 and 2009 using the leaf area index (LAI) as a proxy; 24 measures per plot were taken with a LAI-2000 Plant Canopy Analyzer from LI-COR Biosciences. We confirmed the relationship between LAI and biomass in 8 and 16 plots in 2008 and 2009, respectively. Biomass was measured by cutting and dry-weighing five randomly placed 30 cm  $\times$  30 cm samples in each plot. The resulting Pearson product-moment correlations were 0.89 in 2008 and 0.87 in 2009.

*Potential prey*. In our system, the large majority of prey were pollinators (see Table A2 in Appendix A). Consequently, we estimated the availability of prey by recording insects visiting flowers. This was performed in a subset of six wildflower strips in early August 2008 and 2009, on calm and sunny days between 10:00 and 16:00. In each plot, insects were counted during 15 min in two randomly positioned 1 m  $\times$  1 m plastic frames. All observed individuals ( $>3$  mm in body length) were identified visually at the order level. Potential prey was measured as the total abundance of pollinators in each plot.

*Predators*. Predators of *A. bruennichi* were investigated by direct observations. A single predator, the European hornet *Vespa crabro* L. (Hymenoptera: Vespidae) was detected, easily identified by its characteristic signs of predation (see ‘Results’ section). Due to their large foraging range, the presence or absence of hornets was recorded at the strip level.

## Analyses of *A. bruennichi*’s predation success

At the plot level, a generalized linear mixed effect model with binomial family and logit link function (function *glmer* of package *lme4* in R; Bates and Maechler 2009) was used to investigate the influence of five vegetation characteristics (effective number of species, *Malva* and *Dipsacus* cover, vegetation height and biomass) and of the abundance of potential prey species on the trapping efficiency of *A. bruennichi*. This was performed for the 178 plots where *A. bruennichi* was present. In all analyses using mixed effect models, we used as random factor “block” nested within “wildflower strip”, nested within “year”. We chose this design because the values of all explanatory variables considerably changed from year 2008 to year 2009 (the data do not conform to a standard repeated measures design). Also, as the models with random intercept and random slope often failed to reach convergence, models with random intercept only were used.

At the web level, a linear mixed effect model with Gaussian family and identity link (function *lme* of package *nlme* in R; Pinheiro, Bates, DebRoy, Sarkar, & The R Core Team 2008), with the dependent variable Box–Cox-transformed (Legendre and Legendre 1998), was used to explore the influence of vegetation on the volume of the largest prey. As the latter variable was measured for each web, the plot was added as a random factor nested within “block”.

## Analyses of individual bottom-up and top-down effects on *A. bruennichi*

**Vegetation.** We explored how the three characteristics of vegetation explain the presence/absence and the abundance of *A. bruennichi* in the 216 plots, with generalized linear mixed-effect models (Zuur, Ieno, Walker, Saveliev, & Smith 2009). To select the best model with regard to the fixed effects, we started with a “full” model, which included all five vegetation explanatory variables and their pairwise interactions (higher order interactions were not tested). Variables least affecting the AIC of the model were removed in turn. Once the best model was found, its parameters were estimated with restricted maximum likelihood. Validity of the statistical models was evaluated by visual inspection of the residuals in QQ-plots, and dependent variables were transformed if necessary. For the abundance of *A. bruennichi*, a linear mixed effect model with Gaussian family and identity link was used (function `lme` of package `nlme` in R; Pinheiro et al. 2008), with the dependent variable Box–Cox transformed (Legendre and Legendre 1998). Note that plots without spiders (38 out of 216 plots) were excluded from this analysis. Presence/absence of *A. bruennichi* was analysed with a generalized linear mixed effect model with binomial family and logit link function (function `glmer` of package `lme4` in R; Bates and Maechler 2009).

**Potential prey.** The effect of the total abundance of potential prey on the presence/absence and abundance of *A. bruennichi* was evaluated as above (no model selection was necessary here). This analysis was performed in the four strips (total of 96 plots) where both prey and spiders had been sampled. The total abundance of potential prey was also analysed as a dependent variable to explore the relationships with the characteristics of the vegetation, using the same approach as above.

**Predators.** With the presence of hornets measured at the strip level, the proportional change in the number of spider webs was calculated between 2008 and 2009 for each wildflower strip. The nine wildflower strips were assigned to one of four categories: no hornets present in both years (=“0 → 0”,  $n = 5$ ); hornets present in both years (=“1 → 1”,  $n = 1$ ); hornets only present in 2009 (=“0 → 1”,  $n = 2$ ); and hornets only present in 2008 (=“1 → 0”,  $n = 1$ ). The effect of the presence of hornets on the proportional change (measured as  $\log_2$  of the number of webs in 2009 divided by the number of webs in 2008) in abundance of *A. bruennichi* webs was tested by comparing the categories 0 → 0 and 1 → 1 (no change) vs. 0 → 1 using the one-sided Wilcoxon test.

## Analyses of the organization of bottom-up and top-down effects

The relative importance of the explanatory variables (plant species diversity, plant composition, vegetation structure, abundance of potential prey and presence of predators) on

the abundance of *A. bruennichi* was evaluated within the subset of wildflower strips for which all information was available ( $n = 96$ , with 92 plots where *A. bruennichi* was present). As customarily achieved with path analysis, the aim was to obtain a global view of the factors affecting spider abundance, and to identify direct and indirect interactions. However, given the structure of our experiment with nested random factors, we used a linear mixed effect model (of Gaussian family and random factors as above) after having standardized all variables. Standardization renders the variables dimensionless, and thus the slopes of the linear model can be compared and used as measure of the importance of the “causal” paths. For both plant composition and vegetation structure, a summary variable computed by ordination was used (1st CA and PCA axis, respectively). In this way, all five components were represented by single variables in this global a priori model.

## Results

The abundance of *A. bruennichi* more than doubled between 2008 and 2009, with 917 and 1926 spider webs, respectively. In 2008, a maximum of 4 webs per square metre were observed, while in 2009 densities reached up to 7 webs per square metre. A total of 2083 (2008: 911, 2009: 1172) prey items belonging to 14 different orders were found in *A. bruennichi* webs (Appendix A, Table A2) and the vast majority (95%) were pollinators. The prey community was mostly composed of dipterans (2008: 45%, 2009: 26%) and hymenopterans (2008 and 2009: 35%). About 50% of hymenopterans belonged to the family Apidae.

Plant species were not used as support for webs in proportion to their percentage cover (Appendix A, Fig. A2) ( $\chi^2$  test,  $P \ll 0.001$ ). Two plant species stood out: webs of *A. bruennichi* were disproportionately more often attached to *Malva* sp. (odds ratio 1.72), and less frequently to *D. fullonum* (odds ratio 0.32) than would follow from their density. The percentage covers of these two species were considered as explanatory variables in subsequent analyses describing the effect of plant species composition.

### *A. bruennichi* predation success

In 2008, an average of  $1.63 \pm 1.04$  (mean  $\pm$  s.d.) prey individuals were found per web, while in 2009 this value dropped to  $1.49 \pm 0.85$  (mixed effect model with Poisson distribution: effect of year =  $-0.29$ ,  $z = -5.34$ ,  $P \leq <0.001$ ). Up to eight prey items were found per web, but 56% and 64% of webs contained no prey in 2008 and 2009, respectively ( $G$ -test of independence,  $P < 0.001$ ).

Trapping efficiency was not significantly influenced by the abundance of potential prey, but was affected by vegetation variables. The proportion of webs with prey was higher in plots with tall vegetation (slope = 0.18,  $z = 3.01$ ;  $P = 0.003$ )

and decreased where *Malva* was abundant (slope =  $-0.14$ ,  $z = -2.60$ ;  $P = 0.010$ ). Plant diversity had an effect on trapping efficiency in conjunction with vegetation biomass: it was positive for low vegetation biomass, but disappeared with high biomass (slope of interaction =  $-0.09$ ,  $z = -2.04$ ;  $P = 0.041$ ). It is interesting to note that trapping efficiency was negatively correlated with spider density (Pearson  $r = -0.26$ ,  $t = -3.59$ ,  $P < 0.001$ ).

Prey items were significantly larger for webs in plots with higher plant diversity (d.f. = 881; slope =  $0.286$ ,  $t = 2.137$ ,  $P = 0.033$ ), while in plots with high densities of *Malva*, significantly smaller prey were trapped (estimate =  $-0.322$ ,  $t = -2.278$ ,  $P = 0.023$ ). The structure of the vegetation did not affect prey size.

### Individual bottom-up and top-down effects on *A. bruennichi*

**Vegetation.** The presence or absence of *A. bruennichi* was influenced by plant species diversity, composition and vegetation structure (Table 1). Plant species diversity had a significant positive effect and plots with a higher cover of *Malva* tended to harbour spiders more frequently. However, the height of the vegetation had a negative effect on the presence of *A. bruennichi*. Significant interactions between explanatory variables revealed that (1) high vegetation biomass decreased the negative effect of vegetation height, (2) the abundance of *Malva* reinforced the negative effect of vegetation height, and (3) vegetation biomass reduced the positive effect of *Malva*.

When considering *A. bruennichi* abundance, the only significant direct effect was that fewer webs were found in plots with high abundance of *Dipsacus* (Table 1). Although main effects of *Malva* and of vegetation height were not significant here, they were of the same sign as those for *A. bruennichi* presence/absence.

**Potential prey.** There was a significant positive relationship between potential prey abundance and the presence/absence

of the spider (mixed effect model with binomial response: slope =  $0.98$ ,  $z = 2.70$ ;  $P = 0.007$ ). The effect on spider abundance was also positive, but not significant (slope =  $0.12$ ,  $z = 0.69$ ;  $P = 0.494$ ).

Plant diversity was the only significant factor affecting the abundance of potential prey (slope =  $0.45$ ,  $t = 2.36$ ,  $P = 0.02$ ), while vegetation structure (height: slope =  $0.07$ ,  $t = 0.28$ ,  $P = 0.782$ ; biomass: slope =  $-0.23$ ,  $t = -0.93$ ,  $P = 0.353$ ) and the abundance of *Malva* (slope =  $0.18$ ,  $t = 0.99$ ,  $P = 0.327$ ) and *Dipsacus* (slope =  $-0.31$ ,  $t = -1.57$ ,  $P = 0.119$ ) had no significant effects.

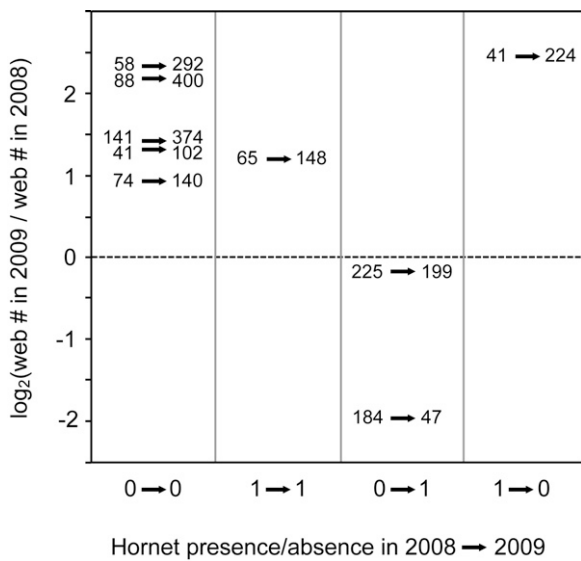
**Predators.** The European hornet *Vespa crabro* was the only species observed attacking *A. bruennichi* on their webs, in the majority of cases pinching off the legs of the spider in order to transport spiders to their nest. We found 64 such events in 2008, and 68 in 2009. Hornets were present in two wildflower strips in 2008, and in three in 2009. Two wildflower strips were newly colonized in 2009 while one was abandoned. The presence of hornets had a strong negative effect on *A. bruennichi* (Fig. 1): their abundance decreased in both wildflower strips with hornets newly present in 2009 (category 0  $\rightarrow$  1), while it increased by a factor of 3.1, on average, in wild-flower strips with no change (categories 0  $\rightarrow$  0 and 1  $\rightarrow$  1). Despite the low sample size, this difference was significant (one-sided Wilcoxon test,  $W = 12$ ,  $P = 0.037$ ). Moreover, the greatest increase in abundance occurred in the wildflower strip abandoned by hornets in 2009.

### Organization of bottom-up and top-down effects

The individual bottom-up and top-down effects on *A. bruennichi* were largely confirmed by our global a priori model (Fig. 2). The strongest numerical effect was that of hornets, followed by vegetation structure, prey community and plant species diversity. With the presence of hornets a marked decrease in spider abundance was observed. Vegetation structure directly affected spider abundance and, as would be expected, the availability of prey directly

**Table 1.** Effect of vegetation characteristics on the presence/absence (no. of observations  $n = 216$ ) and abundance ( $n = 178$ ) of *A. bruennichi* analysed by generalized linear mixed effect models. The results shown here represent the best models obtained by backward elimination. Significant effects are shown in bold; Veg. = vegetation.

Variable	Presence/absence of <i>A. bruennichi</i>				Abundance of <i>A. bruennichi</i>			
	Slope	s.e.	$z$	$P$	Slope	s.e.	$t$	$P$
Plant diversity	0.789	0.318	2.485	<b>0.013</b>				
Vegetation height	$-0.928$	0.351	$-2.649$	<b>0.008</b>	$-0.035$	0.109	$-0.325$	0.746
Vegetation biomass (LAI)					0.185	0.145	1.292	0.199
<i>Malva</i> cover	0.616	0.347	1.776	0.076	0.031	0.088	0.349	0.728
<i>Dipsacus</i> cover					$-0.221$	0.095	$-2.317$	<b>0.022</b>
Veg. height $\times$ Veg. biomass	0.829	0.379	2.185	<b>0.029</b>	0.183	0.094	1.939	0.054
Veg. height $\times$ <i>Malva</i> cover	$-0.917$	0.372	$-2.462$	<b>0.014</b>	0.194	0.092	2.105	<b>0.037</b>
Veg. cover $\times$ <i>Malva</i> cover	$-0.810$	0.346	$-2.340$	<b>0.019</b>				
<i>Malva</i> cover $\times$ <i>Dipsacus</i> cover	0.583	0.301	1.937	0.053	$-0.124$	0.081	$-1.535$	0.127



**Fig. 1.** Change in the abundance of *A. bruennichi* between 2008 and 2009 in relation to the presence (1) or the absence (0) of the hornet *Vespa crabro*. Arrows indicate the change in web abundance between the two years, on a  $\log_2$  scale (i.e., 0 indicates no change, 1 a doubling in abundance,  $-2$  a fourfold decrease) in the nine wildflower strips. Figures on the arrows are the observed number of webs in the two years.

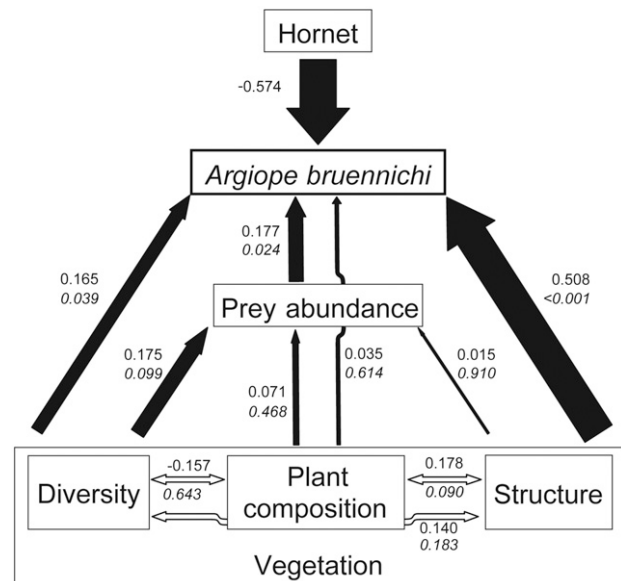
increased the abundance of *A. bruennichi*. Plant species diversity had a direct as well as an indirect effect on the abundance of *A. bruennichi*, by increasing both spider and prey abundance. However, plant composition had neither a direct effect on spiders nor an indirect on prey in our path analysis.

## Discussion

Bottom-up and top-down processes as well as direct and indirect interactions regulate the abundance of *A. bruennichi*. Among the web of interactions found to affect *A. bruennichi*, three factors stood out: the strong negative effect of predatory hornets; the strong direct effect of vegetation structure; and the positive effect of plant species diversity, which affected spider abundance directly and indirectly via potential prey. The latter chain of interaction was expected; however, a direct effect of plant diversity raises interesting questions.

## Predation success

Pollinators, mostly bees, flies and wasps, are the major prey of *A. bruennichi* in our system, which is in line with previous observations (Nyffeler and Benz 1989). Orthopterans, which have sometimes been considered to be an important prey of *A. bruennichi* (Malt 1994), were rare in our wildflower strips, probably because they are infrequent in the



**Fig. 2.** Relative importance of direct bottom-up and top-down effects (black arrows) on the abundance of the web-building spider *A. bruennichi* in 96 plots. “Hornet” was measured as presence/absence; “Diversity” is the effective number of plant species; “Plant composition” is the score of the first CA axis based on the cover of each plant species for each plot; “Structure” is the score of the first PCA axis based on vegetation height and biomass for each plot. Values indicate estimates of standardized slopes, with *P*-values (italic) obtained from linear mixed effect models (note that we provide no *P*-value for the hornet effect because of the strong spatial autocorrelation within strips). White arrows indicate correlations (Pearson *r*, *P*-value in italic) between the different measurements of the plant community.

surrounding matrix of extensive agriculture. We found a negative density-dependent effect of *A. bruennichi* abundance on the number of prey trapped per web. Despite the high abundance of pollinators in wildflower strips (Haaland, Naisbit, & Bersier 2011), prey may become a limiting resource for *A. bruennichi*. In this competition for resources, plant species diversity may become a key factor, since both the abundance of potential prey and prey size increase with plant diversity.

## Bottom-up effects

We observed a tight interaction between vegetation variables and *A. bruennichi* abundance. Vegetation structure was, compared to plant species diversity or plant composition, a better variable to predict the distribution of the spider. As found by Sanders et al. (2008), vegetation height negatively affected the presence of *A. bruennichi*. The importance of vegetation structure for spiders (McNett and Rypstra 2000; Rypstra and Carter 1995) as well as for arthropods in general (e.g., Perner et al. 2005) is well supported. Despite the interest in the relationship between spiders and vegetation structure, few studies have analysed whether this interaction was direct or indirect, acting through its influence on prey

communities (Pearson 2009). Here, we found that vegetation structure significantly influenced spider abundance once all other measured variables had been accounted for, but no evidence of an indirect link was detected.

Plant composition had a strong effect on *A. bruennichi* in our individual analyses of bottom-up and top-down effects. Whereas the presence of *Malva* increased the abundance of our spider, *Dipsacus* negatively affected *A. bruennichi*. This is in line with other studies showing that plant composition affects the abundance of spiders (e.g., Pearson 2009; Schaffers et al. 2008). However, plant composition for the abundance of *A. bruennichi* was not anymore a significant factor in our global path analysis. Here, rather than concentrating on two key plant species, we summarized the overall plant species composition with an ordination method. This discrepancy might consequently be explained by the low variability in overall composition among wildflower strips.

The effect of plant species diversity could be decomposed into a direct and an indirect component, the latter through an increase in both the abundance of potential prey and prey size. Several biodiversity studies have observed a positive relationship between plant diversity and total predator abundance (Haddad et al. 2009; Haddad, Tilman, Haarstad, Ritchie, & Knops 2001; Wenninger and Inouye 2008). For spiders, however, the relationship is less clear since positive (Perner et al. 2005) and negative (Koricheva, Mulder, Schmid, Joshi, & Huss-Danell 2000) interactions have been reported. An indirect effect of plant diversity on *A. bruennichi* is expected, as pollinators – the main prey in our system – are attracted to pollen and nectar rich habitats (Ghazoul 2006; Haaland et al. 2011). Interestingly, our experiment also revealed a direct effect of plant diversity. Three hypotheses have been suggested to explain direct effects of plant diversity on predator diversity (Siemann et al. 1998), all of which might also apply to predator abundance. First, additional resources from a variety of plants may directly increase predator abundance (e.g., pollen and nectar for parasitoids, syrphids, or salticids). However, this is not likely to be the case for web-building spiders. Second, the effect may be apparent through a change in the interaction between pollinators and predators in more diverse habitats, for example if a change in the behaviour of pollinators makes them more easily trapped, irrespective of their abundance. Third, some form of habitat selection on the basis of plant diversity by predators may be a simple and widespread cause for such a direct effect. If predators select habitats with high plant diversity because they generally harbour more prey, a direct effect between plant and predator will be detected when plant diversity and prey abundance are not perfectly correlated. However, habitats may also be selected by spiders for reasons other than prey abundance, for example to enhance trapping efficiency, to obtain protection from predators (Price et al. 1980), or to avoid the negative effect of meteorological conditions (Enders 1975). In any case, the observed direct link between plant diversity and *A. bruennichi* abundance raises questions about plant diversity serving as a cue for habitat selection.

## Top-down effects

The drastic reduction in spider abundance in wildflower strips where hornets were present emphasises that top-down forces are a key factor determining *A. bruennichi* abundance. Even though this effect has a weak statistical significance (due to low sample size at the strip level), we have clear evidence that hornets can have a strong numerical effect. Compared to the bottom-up effects of plants, this factor is, however, not predictable for spiders, since they select their habitat in spring, several months before the main flight period of hornets (late July to August). *A. bruennichi*, like several other web-building spider species, can add secondary structures in the form of irregular tangles of non-sticky silk threads, known as barrier webs, on the plants surrounding their primary web to prevent attacks by predators (Lubin 1975). In our system, such an antipredator measure was commonly observed in one wildflower strip with the strongest predation pressure by hornets in 2009.

## Conclusions

The significant impacts of vegetation characteristics, of prey and of hornets on this intermediate predator support the hypothesis that population abundance of *A. bruennichi* is mediated by both bottom-up and top-down forces. The importance of this combined trophic regulation has been invoked in several models of community organization (Elmhagen and Rushton 2007; Hunter and Price 1992; Oksanen, Fretwell, Arruda, & Niemela 1981). For arthropods, the two modes have been investigated mostly for herbivores (e.g., Cornelissen and Stiling 2009; Denno et al. 2002; Stiling and Rossi 1997), and in a variety of contexts: the importance of seasonality (Gratton and Denno 2003), of spatial variation (Denno, Lewis, & Gratton 2005; Hoekman 2011), or of temperature (Hoekman 2010). More rarely have predatory species been the focus of such research (e.g., Spiller and Schoener 1994), and not within the context of a biodiversity experiment. By quantifying the relative importance of intervening factors, our global approach highlights two non-intuitive results calling for further scrutiny: that spiders, typically studied in their role as predators, are themselves strongly regulated by predation, and that they may respond directly to plant diversity, two questions amenable to manipulative field experiments.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2012.10.001>

## References

- Askenmo, C., von Broemssen, A., Eckman, J., & Jansson, C. (1977). Impact of some wintering birds on spider abundance in spruce. *Oikos*, *28*, 90–94.
- Bates, D., & Maechler, M. (2009). *lme4: Linear mixed-effects models using Eigen and syntax*. R package version 0.999375-31
- Cornelissen, T., & Stiling, P. (2009). Spatial, bottom-up, and top-down effects on the abundance of a leaf miner. *Ecography*, *32*, 459–467.
- Denno, R. F., Gratton, C., Peterson, M. A., Langellotto, G. A., Finke, D. L., & Huberty, A. F. (2002). Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology*, *83*, 1443–1458.
- Denno, R. F., Lewis, D., & Gratton, C. (2005). Spatial variation in the relative strength of top-down and bottom-up forces: Causes and consequences for phytophagous insect populations. *Annales Zoologici Fennici*, *42*, 295–311.
- Elmhagen, B., & Rushton, S. P. (2007). Trophic control of mesopredators in terrestrial ecosystems: Top-down or bottom-up? *Ecology Letters*, *10*, 197–206.
- Enders, F. (1975). Change of web site in *Argiope* spiders (Araneidae). *American Midland Naturalist*, *94*, 484–490.
- Fabian, Y., Sandau, N., Bruggisser, O. T., Kehrl, P., Aebi, A., Rohr, et al. (2012). Diversity protects plant communities against generalist molluscan herbivores. *Ecology and Evolution*, *2*, 2460–2473.
- Foelix, R. H. (2010). *Biology of spiders* (3rd ed.). Cambridge: Harvard University Press.
- Ghazoul, J. (2006). Floral diversity and the facilitation of pollination. *Journal of Ecology*, *94*, 295–304.
- Gratton, C., & Denno, R. F. (2003). Seasonal shift from bottom-up to top-down impact in phytophagous insect populations. *Oecologia*, *134*, 487–495.
- Greenstone, M. H. (1984). Determinants of web spider species diversity: Vegetation structural diversity vs. prey availability. *Oecologia*, *62*, 299–304.
- Haaland, C., Naisbit, R. E., & Bersier, L.-F. (2011). Sown wildflower strips for insect conservation: A review. *Insect Conservation and Diversity*, *4*, 60–80.
- Haddad, N. M., Crutsinger, M. G., Gross, K., Haarstad, J., Knops, J. M. H., & Tilman, D. (2009). Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters*, *12*, 1029–1039.
- Haddad, N. M., Tilman, D., Haarstad, J., Ritchie, J., & Knops, J. M. H. (2001). Contrasting effects of plant diversity and composition on insect communities: A field experiment. *The American Naturalist*, *158*, 17–35.
- Halaj, J., Ross, D. W., & Moldenke, A. R. (1998). Habitat structure and prey availability as predictors of the abundance and community organization of spiders in western Oregon forest canopies. *The Journal of Arachnology*, *26*, 203–220.
- Harwood, J. D., Sunderland, K. D., & Symondson, W. O. C. (2001). Living where the food is: Web location by Linyphiid spiders in relation to prey availability in winter wheat. *Journal of Applied Ecology*, *38*, 88–99.
- Hoekman, D. (2010). Turning up the heat: Temperature influences the relative importance of top-down and bottom-up effects. *Ecology*, *91*, 2819–2825.
- Hoekman, D. (2011). Relative importance of top-down and bottom-up forces in food webs of *Sarracenia* pitcher communities at a northern and a southern site. *Oecologia*, *165*, 1073–1082.
- Hofer, U., Bauer, H., & Bersier, L.-F. (2003). Ecology of three sympatric species of the genus *Chamaeleo* in a tropical upland forest in Cameroon. *Journal of Herpetology*, *37*, 203–207.
- Hunter, M. D., & Price, P. W. (1992). Playing chutes and ladders: Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, *73*, 724–734.
- Jost, L. (2006). Entropy and diversity. *Oikos*, *113*, 363–375.
- Kahmen, A., Perner, J., Audorff, V., Weisser, W., & Buchmann, N. (2005). Effects of plant diversity, community composition and environmental parameters on productivity in montane European grasslands. *Oecologia*, *142*, 606–615.
- Koricheva, J., Mulder, C. P. H., Schmid, B., Joshi, J., & Huss-Danell, K. (2000). Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia*, *126*, 310–320.
- Kumschick, S., Fronzek, S., Entling, M. H., & Nentwig, W. (2011). Rapid spread of the wasp spider *Argiope bruennichi* across Europe: A consequence of climate change? *Climatic Change*, *109*, 319–329.
- Legendre, P., & Legendre, L. (1998). *Numerical ecology*. Amsterdam: Elsevier.
- Lubin, Y. D. (1975). Stabilimenta and barrier webs in the orb webs of *Argiope argentata* (Araneae Araneidae) on Daphne and Santa Cruz Islands, Galapagos. *Journal of Arachnology*, *2*, 119–126.
- Ludy, C. (2007). Prey selection of orb-web spiders (Araneidae) on field margins. *Agriculture Ecosystems & Environment*, *119*, 368–372.
- Malt, S. (1994). Trophische Beziehungen ausgewählter netzbauender Araneen in Halbtrockenrasen unter besonderer Berücksichtigung von *Argiope bruennichi* (Scopoli 1772). *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie*, *9*, 435–446.
- McNett, B. J., & Rypstra, A. L. (2000). Habitat selection in a large orb-weaving spider: Vegetational complexity determines site selection and distribution. *Ecological Entomology*, *25*, 423–432.
- Merrett, P. (1968). The phenology of spiders on heathland in Dorset. Families Lycosidae, Pisauridae, Agelenidae, Mimetidae, Theridiidae, Tetragnathidae, Argiopidae. *Journal of Zoology*, *156*, 239–256.
- Moon, M.-J. (2012). Organization of the spinnerets and spigots in the orb web spider, *Argiope bruennichi* (Araneae: Araneidae). *Entomological Research*, *42*, 85–93.
- Nyffeler, M., & Benz, G. (1978). Prey selection by web spiders *Argiope bruennichi* (Scop), *Araneus quadratus* (Cl), and *Agelena labyrinthica* (Cl) on fallow land near Zurich, Switzerland. *Revue Suisse de Zoologie*, *85*, 747.
- Nyffeler, M., & Benz, G. (1981). Freilanduntersuchungen zur Nahrungsökologie der Spinne: Beobachtungen aus der Region Zürich. *Anzeiger für Schädlingskunde Pflanzenschutz Umweltschutz*, *54*, 33–39.
- Nyffeler, M., & Benz, G. (1989). Foraging ecology and predatory importance of a guild of orb-weaving spiders in a grassland habitat. *Journal of Applied Entomology*, *107*, 166–184.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'Hara, R. G., Simpson, G. L., et al. (2010). *vegan: Community ecology package*. R package version 1.17-0.

- Oksanen, L., Fretwell, S. D., Arruda, J., & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, *118*, 240–261.
- Pearson, D. E. (2009). Invasive plant architecture alters trophic interactions by changing predator abundance and behaviour. *Oecologia*, *159*, 549–558.
- Perner, J., Wytrykush, C., Kahmen, A., Buchmann, N., Egerer, I., Creutzburg, S., et al. (2005). Effects of plant diversity, plant productivity and habitat parameters on arthropod abundance in montane European grasslands. *Ecography*, *28*, 429–442.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & The R Core Team. (2008). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-93.
- Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. N., & Weis, A. E. (1980). Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, *11*, 41–65.
- Prokop, P., & Gryglakova, D. (2005). Factors affecting the foraging success of the wasp-like spider *Argiope bruennichi* (Araneae): Role of web design. *Biologia*, *60*, 165–169.
- R Development Core Team. (2009). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rypstra, A. L., & Carter, P. E. (1995). The web spider community of soybean agroecosystems in southwestern Ohio. *Journal of Arachnology*, *23*, 135–144.
- Sanders, D., Nickel, H., Grutzner, T., & Platner, C. (2008). Habitat structure mediates top-down effects of spiders and ants on herbivores. *Basic and Applied Ecology*, *9*, 152–160.
- Schaffers, A. P., Raemakers, I. P., Sykora, K. V., & Ter Braak, C. J. F. (2008). Arthropod assemblages are best predicted by plant species composition. *Ecology*, *89*, 782–794.
- Siemann, E., Tilman, D., Haarstad, J., & Ritchie, M. (1998). Experimental test of the dependence of arthropod diversity on plant diversity. *The American Naturalist*, *152*, 738–750.
- Spiller, D. A., & Schoener, T. W. (1994). Effects of top and intermediate predators in a terrestrial food web. *Ecology*, *75*, 182–196.
- Stiling, P., & Rossi, A. M. (1997). Experimental manipulations of top-down and bottom-up factors in a tri-trophic system. *Ecology*, *78*, 1602–1606.
- Topping, C. J., & Lövei, G. L. (1997). Spider density and diversity in relation to disturbance in agroecosystems in New Zealand, with comparison to England. *New Zealand Journal of Zoology*, *21*, 121–128.
- Walker, M., & Jones, T. H. (2001). Relative roles of top-down and bottom-up forces in terrestrial tritrophic plant-insect herbivore-natural enemy systems. *Oikos*, *93*, 177–187.
- Walter, A., Westphal, C., Bliss, P., & Moritz, R. F. A. (2011). Drinking behaviour of the orb web spider *Argiope bruennichi* (Araneae; Araneidae). *Behaviour*, *148*, 1297–1311.
- Welke, K. W., & Schneider, J. M. (2010). Males of the orb-web spider *Argiope bruennichi* sacrifice themselves to unrelated females. *Biology Letters*, *6*, 585–588.
- Wenninger, E. J., & Inouye, R. S. (2008). Insect community response to plant diversity and productivity in a sagebrush-steppe ecosystem. *Journal of Arid Environments*, *72*, 24–33.
- Zimmer, S. M., Welke, K. W., & Schneider, J. M. (2012). Determinants of natural mating success in the cannibalistic orb-web spider *Argiope bruennichi*. *PLoS ONE*, *7*, e31389.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R* (1st ed.). New York: Springer.