

## LETTER

# Towards a mechanistic understanding of temperature and enrichment effects on species interaction strength, omnivory and food-web structure

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### Abstract

Revealing the links between species functional traits, interaction strength and food-web structure is of paramount importance for understanding and predicting the relationships between food-web diversity and stability in a rapidly changing world. However, little is known about the interactive effects of environmental perturbations on individual species, trophic interactions and ecosystem functioning. Here, we combined modelling and laboratory experiments to investigate the effects of warming and enrichment on a terrestrial tritrophic system. We found that the food-web structure is highly variable and switches between exploitative competition and omnivory depending on the effects of temperature and enrichment on foraging behaviour and species interaction strength. Our model contributes to identifying the mechanisms that explain how environmental effects cascade through the food web and influence its topology. We conclude that considering environmental factors and flexible food-web structure is crucial to improve our ability to predict the impacts of global changes on ecosystem diversity and stability.

### Keywords

Climate change, enrichment, food-web topology, intraguild predation, metabolic theory of ecology, nonlinear interaction strength, predator–prey interactions.

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## INTRODUCTION

The study of the relationship between species diversity and food-web stability has a long and discordant history in ecology: theory predicts that complex food webs are less stable than simpler ones, whereas stability (i.e. long-term persistence) is often observed in complex ecosystems (Rooney & McCann 2012). Recently, theoretical studies including more realistic models have shown that stability depends on the functional traits of species (e.g. body size, foraging behaviour), species interaction strengths, and food-web structure (McCann *et al.* 1998; Brose *et al.* 2006, 2008; Rooney & McCann 2012). However, the mechanisms linking these three features and the effects of global changes on these links remain little explored. Given the unprecedented rate of species extinctions, revealing the influence of global change drivers on individual species, species interaction strengths, and food-web structure is therefore a crucial step towards a mechanistic understanding of community dynamics and diversity in a changing world.

Increases in resource availability (hereafter, enrichment) and temperature (climate warming) are two major drivers of biodiversity change (Sala *et al.* 2000). They both have important consequences for individuals, populations, and communities (Tylianakis *et al.* 2008), but their interactive effects on the distribution and strength of species interactions in food webs are

barely known. Most empirical studies have examined the impacts of global changes on organism performance, species distribution, and phenology without – until recently – considering trophic interactions (see Tylianakis *et al.* 2008; for a review). This is puzzling because trophic interactions strongly influence the stability of ecosystems and their response to environmental changes (Petchey *et al.* 1999; Stouffer & Bascompte 2010; Rooney & McCann 2012). The aim of this study was thus to investigate the effects of temperature and enrichment on a terrestrial tritrophic food web that includes omnivory (Fig. 1). Omnivory modules are ubiquitous in nature (Polis *et al.* 1989; Arim & Marquet 2004; Stouffer *et al.* 2007) and play a crucial role as they tend to increase food-web stability (Neutel *et al.* 2007) and persistence (Stouffer & Bascompte 2010). Understanding the effects of global changes on omnivory modules is, therefore, of paramount importance when predicting features of future communities.

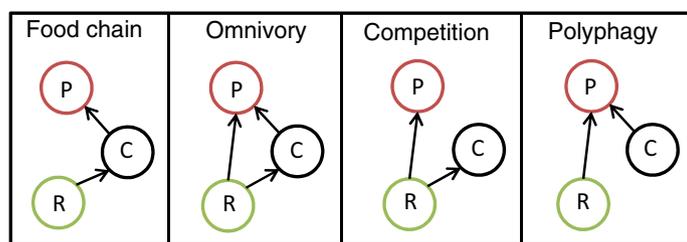
Temperature is one of the most important abiotic factors influencing nearly all metabolic and biological rates, species interactions, population dynamics and ecosystem functioning (Petchey *et al.* 1999; Brown *et al.* 2004; Tylianakis *et al.* 2008), but, surprisingly, its effects on omnivory modules remain unexplored. In simple predator–prey systems, warming typically increases short-term interaction strength (i.e. feeding rate) because predators are more efficient at searching and

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**Figure 1** Diagrammatic representation of the four possible three-species modules that include an omnivore predator (P), an intermediary consumer (C) and a resource (R). Arrows indicate the direction of energy flows from the resource to higher trophic levels.

handling prey (Rall *et al.* 2012; Sentis *et al.* 2012). In complex food webs, a recent theoretical model (Petchey *et al.* 2010) predicts that the effects of warming on food-web connectance (i.e. the relative number of links between species) depends on the relative temperature sensitivities of consumer search rate and handling time: if search rate increases faster with temperature than handling time, consumers would spend relatively more time handling prey and less time searching and thus become more specialised, which would result in a decrease in connectance, and vice versa. Rall *et al.* (2012) recently reported in a meta-analysis that attack rate is generally more sensitive to temperature change than handling time and this, according to Petchey *et al.* (2010), would result in a decrease in connectance with warming. Altogether, this suggests that, in omnivory modules, warming should increase short-term interaction strength and decrease connectance (i.e. omnivory). However, to our knowledge, these predictions remain untested, reflecting an important gap between theoretical and empirical studies.

The effects of enrichment on the persistence of simple food chains and omnivory modules have received considerable attention (Rosenzweig 1971; Holt & Polis 1997; Diehl & Feiszel 2000; Borer *et al.* 2003, 2007). Theory predicts that an omnivore, an intermediate consumer, and their shared resource cannot coexist at a higher enrichment level because the omnivore drives the consumer to extinction through a combination of competition and predation (Holt & Polis 1997). However, this prediction has received only limited empirical support (Morin 1999; Borer *et al.* 2003; Amarasekare 2007, 2008; Novak 2013). Subsequent models showed that weak interaction strength, predator interference, or adaptive foraging can increase the consumer persistence domain (Krivan 2000; Krivan & Diehl 2005), stabilise food webs (McCann & Hastings 1997; McCann *et al.* 1998), and dampen the paradox of enrichment (Rall *et al.* 2008). These studies suggest that omnivore foraging behaviour and species interaction strength are key determinants of the persistence and stability of omnivory modules. We thus argue that investigating how foraging behaviour and species interaction strength are affected by enrichment and warming is an essential step towards a mechanistic understanding of omnivory module stability.

In this study, we combined experimental and modelling approaches to investigate the effects of enrichment and temperature on omnivore foraging behaviour, species interaction

strength and food-web structure (topology) using a plant-aphid-predator mesocosm system. We hypothesised that the effects of temperature and enrichment on the experimental food-web response are driven by the omnivore's behaviour and feeding rate. On the basis of the Petchey *et al.* (2010) model, we expected that if omnivore attack rate is more sensitive to temperature than handling time, connectance (omnivorous link) would decrease with warming. Our model and experiments thus aimed at investigating omnivore response to temperature and enrichment. Furthermore, we measured the effects of temperature and enrichment on the strength of all pairwise interactions to examine how environmental drivers influence food-web structure and dynamics. We found that the structure of the experimental food web is highly dynamic and switches from exploitative competition to omnivory depending on the effects of temperature and enrichment on predator foraging behaviour and species interaction strength. We identified mechanisms underlying experimental patterns that explain how temperature and enrichment effects cascade through the food web and influence its topology. This study shows that environment, foraging behaviour, species interaction strength, and community structure are tightly linked and dynamic. It emphasises the importance of considering environmental factors and flexible food-web structure in future studies to understand and predict relationships between diversity and stability.

## MATERIALS AND METHODS

### Biological system

The tritrophic food web under study consisted of the spotted ladybeetle *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae) as omnivorous predator, the predatory midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) as consumer and the green peach aphid *Myzus persicae* Sulzer (Homoptera: Aphididae) as resource. These three insect species share similar habitats (i.e. host plants) and coexist in nature (Boiteau 1983). Ladybeetle larvae are generalist predators that actively search for prey while *A. aphidimyza* larvae are furtive predators specialised on aphids that spend their entire immature development stage within a prey colony and do not elicit significant defensive reactions from aphids (Lucas & Brodeur 2001). In this system, *C. maculata* is the top predator since *A. aphidimyza* cannot feed on it (Lucas & Brodeur 2001). Aphid colonies are exploited by a large number of predators, and trophic omnivory is very common among aphidophagous predators and parasitoids (Brodeur & Rosenheim 2000; Gagnon *et al.* 2011). Aphids and their predators therefore constitute an excellent biological model to explore the effects of temperature and enrichment on short-term interaction strength and community structure.

### Model

The nonlinear functional response (Holling Type II) adequately describes the relationship between feeding rate (i.e. short-term interaction strength) and prey density for most predators, including *C. maculata* (Sentis *et al.* 2012). Rogers

(1972) proposed a modification of the disc equation (Holling 1959) that takes into account prey depletion:

$$N_e = N_0(1 - e^{-a(t-hN_e)}), \quad (1)$$

where  $N_e$  is the number of prey eaten,  $N_0$  the initial density of prey (units: prey area<sup>-1</sup>),  $t$  the total experimental time,  $a$  the search rate (searching efficiency of the predator; units: area time<sup>-1</sup>) and  $h$  the handling time (time to attack, kill, and eat a prey; units: time prey<sup>-1</sup>). The reciprocal value of the handling time parameter corresponds to the maximum feeding rate, which is approached asymptotically as prey density increases.

Following Lawton *et al.* (1974), we extended eqn 1 to predict the number of resources and consumers eaten by the omnivore,  $N_R$  and  $N_C$  respectively:

$$N_R = N_{0R}(1 - e^{-a_R(t-h_R N_R - h_C N_C)}) \quad (2)$$

$$N_C = N_{0C}(1 - e^{-a_C(t-h_C N_C - h_R N_R)}), \quad (3)$$

where the subscripts  $R$  and  $C$  refer to resource and consumer respectively. We assumed that the effect of the consumer on resource density is negligible in our biological system because the consumer (*A. aphidimyza*) feeding rate is very low (from 1 to 3 aphids per day), and this simple model fits the experimental observations well (Sentis *et al.* 2013).

Because *A. aphidimyza* larvae live within the aphid colony and remain immobile for long periods (as aphids do), we assumed a similar search rate for *C. maculata* exploiting either resource or consumer (i.e.  $a_R = a_C$ ). Setting  $a_R = a_C$  in eqn 3 yields:

$$N_C = N_{0C}(1 - e^{-a_R(t-h_C N_C - h_R N_R)}). \quad (4)$$

Equation 4 represents a null model where the predator has no preference for a particular prey or switches from one prey to the other.

Foraging traits such as search rate and handling time can be related to temperature using the metabolic theory of ecology (MTE) developed by Brown *et al.* (2004). Based on MTE, handling time depends on body mass ( $M$ , in mg) and environmental temperature ( $T$ , in K) as follows:

$$h(T) = h_0 M^{b_h} e^{\frac{E_h}{kT}}, \quad (5)$$

where  $h_0$  is a normalisation constant independent of body size and temperature,  $b_h$  an allometric exponent,  $E_h$  the activation energy (0.65 eV; Brown *et al.* 2004) and  $k$  the Boltzmann's constant ( $8.62 \times 10^{-5}$  eV K<sup>-1</sup>). The value of  $b_h$  is assumed to be 0.75 and is derived from the physics of distribution networks in animals (Brown *et al.* 2004).

In a previous study (Sentis *et al.* 2012), we found that the relationship between temperature and search rate for *C. maculata* preying on *M. persicae* deviates significantly from the form of eqn 5. We, therefore, used the following model that accounts for nonlinearity:

$$a(T) = b(T - T_0)(T_l - T)^{\frac{1}{2}}, \quad (6)$$

where  $a(T)$  is a positive function of temperature,  $b$  an empirical constant and  $T_l$  and  $T_0$  the upper and lower thresholds for search rate respectively. In addition, we set  $a(T)$  equal to zero

for  $T \leq T_0$  and  $T \geq T_l$  because search rate cannot be negative.

Inserting eqns 5 and 6 into the model (eqns 2 and 4) yields the following temperature-dependent model:

$$N_R = N_{0R}(1 - e^{-a_R(T)(t-h_R(T)N_R-h_C(T)N_C)}) \quad (7)$$

$$N_C = N_{0C}(1 - e^{-a_R(T)(t-h_C(T)N_C-h_R(T)N_R)}). \quad (8)$$

Equations 7 and 8 predict the number of resources and consumers eaten, respectively, by the omnivorous predator as a function of temperature and both resource and consumer densities. The package "EMDBOOK" was used to solve recursive functions 7 and 8 with the Lambert W function (see Appendix A in Sentis *et al.* 2013 for details). Models were developed using R software (version 2.13.1; R Development Core Team 2011).

#### Parameter selection

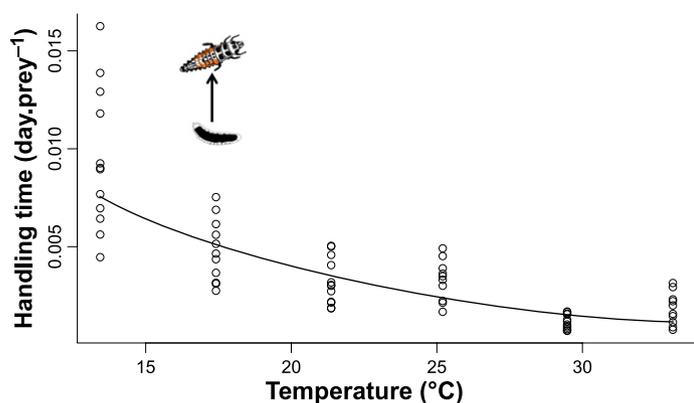
To generate model predictions for our experimental biological system, only three temperature-dependent functions are needed: handling time for the consumer,  $h_C(T)$ , search rate for the resource,  $a_R(T)$  and handling time for the resource,  $h_R(T)$ . The first function,  $h_C(T)$ , was estimated from experiment 1. For the two other functions, we used data from Sentis *et al.* (2012), where we measured the functional response of *C. maculata* preying on *M. persicae* across a large gradient of temperatures (13.9–32.8 °C), and used the Rogers random predator equation (1972) to estimate handling time and search rate values at each of the six experimental temperatures. In this study, the MTE equation (eqn 5) was fitted to the handling time data from Sentis *et al.* (2012) using a log-linear regression. For the search rate, we first fitted the hump-shaped equation (eqn 6) to the data from Sentis *et al.* (2012) using a nonlinear least-square regression. Following the approach of Dell *et al.* (2011), we next excluded the search rate value for the highest temperature (32.8 °C) to focus on the rising part of the curve (search rate decreases above 30 °C; Fig. 2b in Sentis *et al.* 2012). This approach allows the estimation of the activation energy ( $e$ ) for the search rate by fitting the MTE equation (eqn 5) to the data using a log-linear regression. We next compared the absolute value of handling time and search rate activation energies, and used the model of Petchey *et al.* (2010) to predict the effects of temperature on connectance in our experimental food web.

## EXPERIMENTS

The experiments aimed at: (1) estimating model parameters (experiment 1), (2) testing model predictions (experiment 2) and (3) investigating the effects of temperature and enrichment on the strength of all pairwise interactions in the experimental food web (experiment 2).

#### Insect rearing and standardisation for experiments

Experiments were conducted using insects from two-year-old laboratory cultures. Aphids were maintained on sweet pepper (*Capsicum annum* L. cv. Bell Boy), and predators were fed aphids and pollen *ad libitum*. All insects and plants were



**Figure 2** Relationship between temperature and handling time for *Coleomegilla maculata* preying on *Aphidoletes aphidimyza*. The model equation is  $h_{ig}(T) = 7.64 \times 10^{-16} M^{0.75} e^{0.71/kT}$ , where  $M$  is the predator body mass (4.71 mg),  $T$  (K) is the environmental temperature and  $k$  is the Boltzmann's constant ( $8.62 \times 10^{-5}$  eV  $K^{-1}$ ) ( $r^2 = 0.67$ ,  $P < 0.0001$ ,  $n = 67$ ). In the insect pictogram, the arrow indicates the direction of energy flow from consumer (*A. aphidimyza*) to omnivore (*C. maculata*).

reared in a growth chamber (Conviron<sup>®</sup> E15, Controlled Environments, Inc., Winnipeg, Manitoba, Canada) at  $24 \pm 1$  °C, a light intensity of  $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ , and under a 16L:8D photoperiod. Sentis *et al.* (2013) provide additional information on the origin of the insects and rearing procedures. For both experiments, we used *M. persicae* 3rd instar larvae (mean weight  $\pm$  SE:  $0.17 \pm 0.025$  mg) and *C. maculata* 3rd instar larvae ( $4.71 \pm 2.28$  mg) reared from synchronous cohorts. Because a controversy exists about the number of *A. aphidimyza* larval instars (Lucas *et al.* 1998), we standardised tested predatory midge larvae based on their age (72 h after hatching) and size (length: 1.3 mm). During experiments, temperature and humidity ( $70 \pm 8\%$ ) were recorded continuously using Hobo U12 (Hobo<sup>®</sup>, Bourne, MA, USA) units placed in the experimental arenas.

#### Experiment 1: handling time for the consumer as a function of temperature $h_c(T)$

This experiment was designed to estimate the handling time for *C. maculata* preying on *A. aphidimyza* at six temperatures (14, 18, 22, 26, 30 and  $34 \pm 1$  °C). An *A. aphidimyza* larva was isolated in a Petri dish ( $40 \times 12$  mm) and allowed to acclimatise to experimental conditions for 30 min. A *C. maculata* larva was then introduced into the Petri dish and its activity was recorded with an HD camera (Sony HDR-XR500<sup>®</sup>, Tokyo, Japan). We next examined videos to measure handling time, which was defined as the time interval from the beginning of an attack to the moment when *C. maculata* finished eating *A. aphidimyza*. In all replicates, no attack failed and *C. maculata* never moved away before entirely consuming its prey. We conducted 12 replicates per temperature. The MTE equation (eqn 5) was fitted to the data using a log-linear regression. We next inserted the estimated parameters into the model (eqns 7 and 8) to generate predictions.

#### Experiment 2: effects of temperature and enrichment on interaction strength

This experiment aimed at recording the effects of temperature, enrichment and their interaction on the pairwise interaction strength within the omnivory module. The experiment had a fully factorial design with three temperatures (14, 22, and  $30 \pm 1$  °C) and three enrichment levels (10, 45, and 90 aphids). Experimental arenas consisted of a plastic cylinder ( $\emptyset$ : 20 cm, height: 45 cm) in which 4-week-old sweet pepper plants were individually enclosed. Chosen densities of aphids were then transferred to the upper leaves of the plant and, after 1 h of acclimation, an *A. aphidimyza* larva was placed near the aphid colony. Thirty minutes later, a *C. maculata* larva was introduced at the bottom of the stem. After 24 h, we recorded insect numbers. We were able to distinguish aphids eaten by either *C. maculata* or *A. aphidimyza* because the latter extract aphid body contents, leaving an empty exoskeleton (Lucas *et al.* 1998) that is not eaten by *C. maculata* (A. Sentis, personal observation). Fifteen replicates of the omnivory treatment (*M. persicae* + *A. aphidimyza* + *C. maculata*), five replicates of the treatment without *C. maculata* (*M. persicae* + *A. aphidimyza*) and four replicates of the control treatment without predators (*M. persicae* only) were performed for each temperature–density combination.

A binomial GLM with a logit link function was used to test the effects of enrichment, temperature, and their interaction on the proportion of aphids killed by the omnivorous predator (*C. maculata*). We detected model overdispersion and thereby corrected the standard errors using a quasi-GLM model (Zuur *et al.* 2009). An analysis of deviance was subsequently performed using an F-test. The effects of temperature, enrichment and their interaction on the proportion of *A. aphidimyza* eaten by *C. maculata* were tested with a binomial GLM with a logit link. This model was not overdispersed, and the analysis of deviance was thereby performed using a chi-squared test (Zuur *et al.* 2009). Following McCann *et al.* (1998; Box 1, eqn 3), we defined the *per capita* interaction strength,  $IS_{ji}$ , of resource species  $i$  on consumer species  $j$  as:

$$IS_{ji} = \frac{F_j(N_i)}{N_i}, \quad (9)$$

where  $F_j(N_i)$  is the predation rate (prey  $\text{day}^{-1}$ ) of consumer  $j$  on resource  $i$  and  $N_i$  is the resource density. Equation 9 was used to calculate the empirical interaction strength for each pairwise interaction. Data were analysed using R software (v. 2.13.1; R Development Core Team 2011).

## RESULTS

### Model parameters

As predicted by MTE, we found that handling times for both consumer (experiment 1) and resource (data from Sentis *et al.* 2012) decrease exponentially with temperature (for consumer:  $h_c(T) = 7.64 \times 10^{-16} M^{0.75} e^{0.71/kT}$ ;  $r^2 = 0.67$ ,  $P < 0.0001$ ,  $n = 67$ ; Fig. 2, and for resource:  $h_R(T) = 5.38 \times 10^{-14} M^{0.75} e^{0.68/kT}$ ;  $r^2 = 0.89$ ,  $P < 0.0001$ ,  $n = 6$ ) and our estimates of energy activation ( $0.71 \pm 0.06$  eV for consumer and

$0.68 \pm 0.1$  eV for resource) correspond well to the value expected by MTE (0.65 eV; Brown *et al.* 2004). In contrast, the relationship between temperature and search rate (data from Sentis *et al.* 2012) was better described by a hump-shaped equation:  $a_R(T) = 0.08 (T-285.7) (308.8-T)^{1/2}$ ;  $r^2 = 0.88$ ,  $P < 0.0001$ ,  $n = 6$ . When we excluded search value for the highest temperature (32.8 °C) and fitted the MTE equation to the data, we found that, as predicted by MTE, search rate increases exponentially with temperature ( $a_R(T) = 9.86 \times 10^{12} M^{0.75} e^{-0.77/kT}$ ;  $r^2 = 0.93$ ,  $P < 0.0001$ ,  $n = 5$ ). However, the estimate of energy activation ( $-0.77 \pm 0.1$  eV) was higher than the value expected by MTE (0.65 eV). Finally, we found that the absolute values of the activation energies were lower for handling times (0.71 and 0.68 eV for consumer and resource respectively) than for the search rate (0.77 eV), which suggests that, according to Petchey *et al.* (2010), warming should decrease connectance in our experimental food web.

### Model predictions

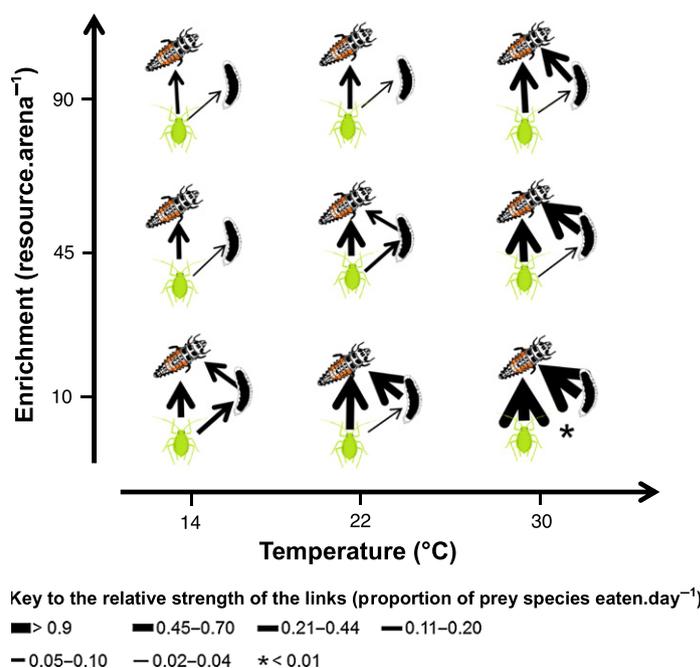
The equations for search rate,  $a_R(T)$ , resource handling time,  $h_R(T)$  and consumer handling time,  $h_C(T)$ , were substituted into eqns 7 and 8 to generate predictions about the number of resources (*M. persicae*) and consumers (*A. aphidimyza*) eaten by the omnivore (*C. maculata*). Following eqn 7, the number of resources eaten by the predator increases with both enrichment and temperature but decreases rapidly at extreme temperatures (>30 °C; Fig. S1). Following eqn 8, omnivory strength decreases with enrichment and increases with temperature, but decreases rapidly at extreme temperatures (>30 °C; Fig. S2) because of the hump-shaped relationship between temperature and search rate. This predicted decrease in omnivory strength was not empirically tested because the warmest experimental temperature was 30 °C.

When comparing model predictions and empirical observations, we assumed that a model prediction is valid when the 95% confidence intervals (CI) of the model prediction overlap with the empirical observation. We calculated the 95% CI of model predictions using the standard errors associated with the estimates of each model parameter and the law of propagation of uncertainty, which is based on a first-order Taylor series expansion error (Rice 2007).

### Experiment 2: effects of temperature and enrichment on interaction strength

Only  $0.5 \pm 0.1\%$  of the aphids died in the treatment without predators, and mortality did not differ between temperatures (Wilcoxon:  $\chi^2 = 8.5$ ,  $df = 5$ ,  $P = 0.13$ ). None of the *A. aphidimyza* (in the treatment without *C. maculata*) or *C. maculata* died during the experiment. As a result, we did not correct for natural aphid and *A. aphidimyza* mortality in our analyses.

The strength of the omnivore–resource and omnivore–consumer interactions increased and decreased with temperature and enrichment respectively (Fig. 3). The strength of the consumer–resource interaction decreased with temperature at low enrichment level, was not affected by temperature at the higher enrichment level, and was higher at 22 °C compared to 14 and 30 °C at the intermediate enrichment level (Fig. 3). Food-web

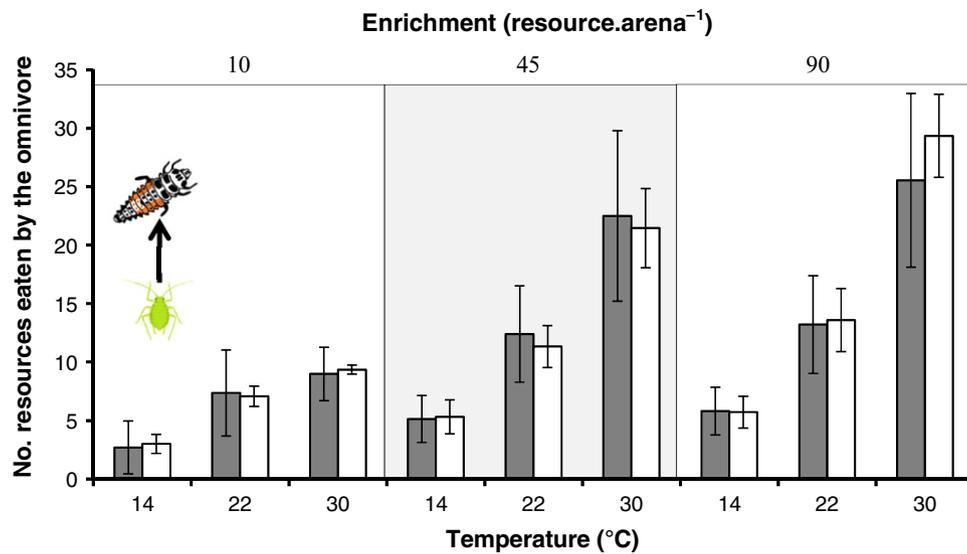


**Figure 3** Interaction webs as a function of temperature and enrichment. The positions of the predators in the webs are ranked vertically. Arrows indicate the direction of energy flows from the resource to higher trophic levels. Arrow width is proportional to interaction strength. Empirical interaction strengths were calculated using eqn 9.

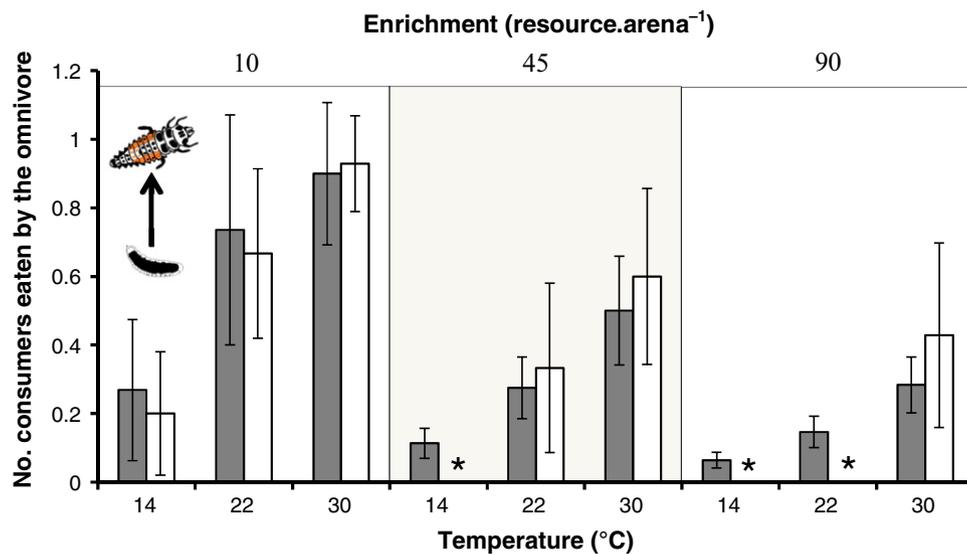
topology was dependent on environmental conditions: we found exploitative competition at low temperature and high enrichment and omnivory at higher temperature and lower enrichment levels (Fig. 3). The three-species module was even very close to polyphagy (i.e. no link between consumer and resource; see Fig. 1) at the lowest enrichment level and highest temperature.

As predicted by the model (eqn 7), the number of resources (aphids) eaten by the omnivore (*C. maculata*) increased significantly with both enrichment and temperature (Fig. 4) (temperature:  $F_{1,128} = 241.7$ ,  $P < 0.0001$ ; enrichment:  $F_{1,127} = 165.6$ ,  $P < 0.001$ ), and the effect of temperature was independent of enrichment level (interaction temperature  $\times$  enrichment:  $F_{1,126} = 0.03$ ,  $P = 0.86$ ). Moreover, for each enrichment–temperature combination, the prediction (eqn 7) fits the empirical observation (Fig. 4).

As predicted by the model (eqn 8), the number of consumers eaten by the omnivore (omnivory strength) increased with temperature ( $\chi^2 = 34.06$ ,  $df = 1$ ,  $P < 0.0001$ ,  $n = 130$ ; Fig. 5) and decreased with enrichment ( $\chi^2 = 29.17$ ,  $df = 1$ ,  $P < 0.0001$ ,  $n = 130$ ). The effect of temperature was independent of enrichment level (interaction temperature  $\times$  enrichment:  $\chi^2 = 1.56$ ,  $df = 1$ ,  $P = 0.21$ ,  $n = 130$ ). The prediction derived from eqn 8 fits the empirical observations well for enrichment levels of 10 and 45 resources per arena (Fig. 5). However, the model predicts non-zero omnivory at 22 °C for high enrichment (i.e. 90 resources per arena) and at 14 °C for intermediate and high enrichment levels (i.e. 45 and 90 resources per arena respectively), but we observed no omnivory in these treatments (Figs 3 and 5).



**Figure 4** Mean number ( $\pm$  95% CI) of resources (*Myzus persicae*) eaten by omnivores (*Coleomegilla maculata*) as a function of enrichment (resource.arena<sup>-1</sup>) and temperature (°C). Open and solid bars represent empirical observations and model predictions (eqn 7) respectively. In the insect pictogram, the arrow indicates the direction of energy flow from resource to omnivore.



**Figure 5** Mean number ( $\pm$  95% CI) of consumers (*Aphidoletes aphidimyza*) eaten by omnivores (*Coleomegilla maculata*) as a function of enrichment (resource.arena<sup>-1</sup>) and temperature (°C). Open and solid bars represent empirical observations and model predictions (eqn 8) respectively. Stars represent treatments for which omnivory did not occur. In the insect pictogram, the arrow indicates the direction of energy flow from consumer to omnivore.

## DISCUSSION

Omnivory plays a crucial role in the dynamics of complex food webs by tending to increase their stability (Neutel *et al.* 2007) and persistence (Stouffer & Bascompte 2010). Here, we found that the omnivory module's topology strongly depends on the effects that temperature and enrichment had on the foraging behaviour and strength of species interactions. By combining modelling and experimental approaches, we identified mechanisms by which both environmental factors cascade through the food web. Our simple model predicts well the observed empirical patterns and can be extended to investigate the effects of environmental drivers on interaction strength

and population dynamics in omnivory modules and more complex food webs. Our results have several implications for the stability of omnivory modules and complex food webs, as discussed below.

As reported in recent empirical studies (Rooney & McCann 2012; Novak 2013), we observed that short-term interaction strength and connectance decrease with enrichment. Our model shows that this general trend is explained by simple density-dependent consumption: the proportion of resource and consumer eaten by the omnivore decreases with resource availability because feeding rate is nonlinear and reaches a maximum at higher prey density. However, we found a lower incidence of omnivory than expected at higher enrichment lev-

els, suggesting that additional mechanisms cause deviations between model predictions and experimental observations. Deviations from null models (without prey switching or prey preference) are common in two-prey/one-predator experiments and generally arise through optimal foraging by predators or adaptive responses by prey to predators (Valdovinos *et al.* 2010; Kalinkat *et al.* 2011). Lucas *et al.* (1998), Lucas & Brodeur (2001) demonstrated that *A. aphidimyza* benefits from a dilution effect generated by its prey when aphids are abundant, which reduces the incidence of trophic omnivory. This probably explains model deviations at higher enrichment levels, but we cannot exclude the possible influence of omnivore foraging behaviour. Whatever the exact process, we found that the omnivore diet switches along the enrichment gradient, which contributes to explaining why the food-web module shifts from omnivory to exploitative competition when enrichment increases.

While several mechanisms have been proposed to explain the ubiquity of omnivory across ecosystems and taxa [see (Kratina *et al.* 2012) for a review], virtually nothing is known about the effects of temperature on omnivory and related consequences for food-web persistence. Our results show that warming increases the strength of species interactions, including omnivory. Our model revealed that the overall impact of temperature on the simple food web is mediated by a direct effect on predator foraging activities: omnivore handling time decreases and search rate increases with temperature (Fig. 2 and Sentis *et al.* 2012). As a result, warming favours encounters and predation of both resources and consumers by omnivores (Figs 3, 4 and 5). Because strong trophic interactions tend to destabilise food webs (McCann *et al.* 1998; Neutel *et al.* 2007; Ruokolainen & McCann 2013), warming could decrease the persistence of omnivory modules and thus complex food webs. On the other hand, we found that cooler temperatures weaken trophic interactions, which could increase food-web persistence. As temperature can fluctuate greatly over short time scales and because ectotherms are highly sensitive to temperature and have specific thermal optima (Brown *et al.* 2004), we thereby expect temperature to play a crucial role in the persistence of omnivory modules and explain part of the discrepancy between theory and data.

In agreement with a recent meta-analysis (Rall *et al.* 2012), we found that search rate is more sensitive to temperature than handling time (i.e. the absolute value of the activation energy is higher for search rate than for handling time). According to Petchey *et al.* (2010), this would result in a decrease in connectance because consumers would spend relatively more time handling prey and less time searching, and thus become more specialised. However, contrary to the prediction of Petchey *et al.* (2010), we observed an increase in connectance – the food web gradually switched from exploitative competition to omnivory – with warming, which, based on our model and data, is explained by the increase in feeding rate and interaction strength with warming. Following population dynamics models (McCann & Hastings 1997; McCann *et al.* 1998; Ruokolainen & McCann 2013), our results indicate that warming could decrease the stability of omnivory modules because strong interaction strength and high connectance tend to destabilise biological networks. Interestingly, we

observed that enrichment decreases species interaction strength, which should dampen the destabilising effect of warming. Because enrichment is predicted to increase in the next few decades (Sala *et al.* 2000), the consequences of global changes on omnivory should then depend on the relative increase in enrichment and temperature: if enrichment increases faster than temperature, omnivory interactions would be weaker and vice versa.

Theoretical models predict that coexistence in omnivorous modules depends on the strength of both omnivory and omnivore–consumer competition for exploiting the resource (Holt & Polis 1997; McCann *et al.* 1998; Mylius *et al.* 2001). Along with these concepts, one can use our empirical measures of interaction strength to forecast how module stability would be affected by different levels of temperature and enrichment. At low enrichment and high temperature (Fig. 3), the omnivore is a strong competitor and predator, which should lead to instability (McCann *et al.* 1998; Mylius *et al.* 2001). At high enrichment and low temperature, the system is dominated by exploitative competition, which should lead to the exclusion of the weakest competitor. Therefore, coexistence seems only possible for intermediate levels of enrichment and temperature. However, in the long term, these predictions would also depend on the predator's metabolic response to warming (Rall *et al.* 2010; Binzer *et al.* 2012): if basal metabolic rate increases faster with temperature than feeding rate, the predator's energetic budget and then average predator abundance (or biomass) would decrease and thus stabilise the system dynamics, or vice versa. In any case, these predictions hold true only if we assume that environmental drivers remain constant, which is unlikely under natural conditions. If temperature and resource density fluctuations induce rapid changes in food-web structure and decrease the overall interaction strength, then environmental variations could be a strong driver for species coexistence, as suggested by recent theoretical studies (Vasseur & Fox 2007; Ruokolainen & McCann 2013).

## CONCLUSION

Natural habitats are characterised by short-term variations and long-term trends in environmental conditions, which can both influence species interaction strength and food-web dynamics. However, many theoretical studies assume that environment, organism behaviour, species interaction strength, or food-web structure (or topology) are static (Holt & Polis 1997; McCann & Hastings 1997; McCann *et al.* 1998; Neutel *et al.* 2007). Such simplifications are useful when classifying the nature of ecological interactions (e.g. predation, competition) and generating simple models, but they mostly ignore the dynamic aspect of food webs. Here, we demonstrate that organism behaviour, species interaction strength, and food-web topology strongly depend on environmental drivers. Our results show that enrichment decreases species interaction strength and the occurrence of omnivory, which causes the food web to gradually shift from omnivory to exploitative competition. However, warming leads to the opposite effect by increasing species interaction strength which, in the longer term, could destabilise the network. By scaling up from indi-

vidual behaviour to community, we have identified some determinant links between organism behaviour, interaction strength, and food-web structure. This suggests that taking into account these links is a crucial step towards a mechanistic understanding of the effects of environmental variations on omnivory modules. Given the importance of omnivory modules for the stability of complex food webs (Stouffer & Bascompte 2010), our findings have implications for the diversity–stability relationship.

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#### AUTHOR CONTRIBUTIONS

A.S., J.L.H. and J.B. conceived and designed the experiments. A.S. performed modelling work and experiments, and analysed the data. A.S. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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