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Conserving species-rich predator assemblages strengthens natural pest control in a climate warming context

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Abstract

1 Recent evidence has shown that a consideration of multiple drivers is important if we want to understand how ecosystem functioning will respond to global change.

2 In the present study, we used a substitutive approach to examine how two major components of global change, warming and predator diversity, affect the top-down control of two phytophagous insect pests. Predator assemblages were created using a substitutive design to give three single-species treatments (low diversity) and one three-species treatment (high diversity) under two temperature treatments (current seasonal temperature and an increase of +3°C over current temperatures).

3 The results obtained indicate a shift from substitutive to complementarity effects among predatory species with experimental warming. Experimental warming revealed complementarity between the predatory species in diverse assemblages because higher predation rates on both prey species were found in the high diversity treatment compared with what was expected based on low diversity treatments at the same temperature.

4 Our analyses of prey selectivity provided evidence that resource-niche partitioning is involved in the emergence of functional complementarity under warming. The present study highlights the importance of maintaining diverse predator assemblages if we want to increase natural pest control services in agroecosystems and reduce dependence on agrochemicals in a climate change context.

Keywords Agroecosystems, biodiversity, biodiversity-ecosystem functioning, climate change, food web, grapevine, multiple predator, trophic cascade.

Introduction

The effects of global environmental changes are predicted to become more important in the future, such as increases in temperature and atmospheric CO_2, as well as losses of biodiversity or biological invasions that are triggered and maintained by human activities (Tylianakis *et al.*, 2008). Several studies have revealed that global environmental changes can affect the geographical distribution and community composition of plant and animal communities (Tylianakis *et al.*, 2008; Sarmento *et al.*, 2010; Walther, 2010; Harley, 2011). These modifications are predicted to alter direct and indirect interactions among species and therefore ecosystem functioning (Tylianakis *et al.*, 2008). However, the empirical evidence related to such effects remains limited (Dossena *et al.*, 2012; Barton & Ives, 2014).

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Changes in abiotic conditions such as temperature affect the strength of trophic interactions that play critical roles in the functioning of terrestrial ecosystems (Schmitz, 2003; Barton *et al.*, 2009; Barton & Ives, 2014). Temperature affects seasonal phenology, metabolic rate or the behaviour of arthropod predators, with potential important consequences related to the top-down control of herbivores and primary producers (Schmitz & Barton, 2014). Moreover, empirical studies have reported that direct effects of predators on herbivores may be reduced at elevated temperatures (Barton, 2010; Laws & Joern, 2013) and also that cascading effects related to invertebrate predators on plant communities can be magnified at elevated temperatures (Barton & Schmitz, 2009; Barton *et al.*, 2009). Furthermore, laboratory and modelling studies have found higher feeding rates and short-term *per capita* interaction strength between predators and their prey at higher temperature, suggesting a higher level of top-down control at higher temperatures (Rall *et al.*, 2010;

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Vucic-Pestic *et al.*, 2011). This variability of outcomes suggests a high context-dependency of trophic interaction responses to elevated temperature, where some interactions are magnified under warming, whereas others are weakened. Moreover, because species differ greatly in their thermal tolerance and because increased temperatures affect foraging, consumption and digestion, as well as growth rates of both predators and prey, warming is assumed to potentially alter the relative strengths of top-down and bottom-up effects in an ecosystem (Hoekman, 2010).

Both diversity and community composition of predators can influence the magnitude of top-down control in different ways. First, a large body of work related to biodiversity and ecosystem functioning suggests that a higher predator diversity leads to an increase in overall predation rates caused by niche partitioning, facilitation or a higher probability of having efficient predators included in the community as the number of species increases (Letourneau *et al.*, 2009; Cardinale *et al.*, 2012). Second, empirical evidence indicates that increasing predator diversity may lead to various effects on the extent of top-down control. Studies have found reduced top-down control as a result of negative interactions among predators such as intraguild predation (Martin *et al.*, 2013). Other studies have reported a similar level of top-down control at a different level of predator diversity caused by the balance between positive and negative interactions (Straub *et al.*, 2008; Letourneau *et al.*, 2009). Finally, recent studies have demonstrated that important functional traits, such as hunting-mode, relative body size or habitat domain of predator and prey, are good predictors of the rate of top-down control of herbivores by their natural enemies (Schmitz, 2008; Schneider *et al.*, 2012; Rusch *et al.*, 2015).

Biodiversity loss is a major component of global change (Hooper *et al.*, 2012). Declines in biodiversity over time have been observed for many different communities, including natural enemies of crop pests because of changes in climate, land use or farming practices (Robinson & Sutherland, 2002; Thomas *et al.*, 2004). However, the way that predator diversity will affect top-down control in agroecosystems remains poorly understood (Letourneau *et al.*, 2009). There is increasing concern that studies investigating the consequences of individual components of global change may not reflect their synergistic or antagonistic joint effects in real ecosystems or ecological communities (Didham *et al.*, 2007; Tylianakis *et al.*, 2008; Hoover *et al.*, 2012; Rosenblatt & Schmitz, 2014). Complex interactions between multiple drivers of global change provide an important reason for considering more than one driver if we are to understand how ecosystem functioning will respond to global change.

In the present study, we examined how experimental warming and reduced predator diversity affect the predation of two phytophagous pests using a substitutive approach. The present study used representative assemblages of predator and prey species found in agroecosystems that were observed to differ in their functional traits. We hypothesized that the emergent effect of multiple predator species assemblages on predation rates is determined by the habitat domain of both predator and prey (Schmitz, 2007). We selected three predatory species that show complementarity in their habitat domain either in time (nocturnal vs. diurnal species) or in their hunting mode (sit-and-wait vs. active hunter predators). We hypothesized that a substitutable effect (linear average of single species effects) of predatory species will occur in the ambient temperature treatment because the complementary habitat domain limited interspecific interactions between predators. We expected that the warming effect on predators and prey will affect the feeding niche of predators and modify the emergent effects of multiple assemblages on predation rates from the substitutable effect to either risk reducing or risk enhancement for the prey. We also expected higher predation rates by individual predatory species in the elevated temperature treatment compared with ambient temperature as a result of accelerated metabolism.

Materials and methods

Study system

We selected grapevine (*Vitis vinifera*) to test our hypotheses for several reasons. First, various pests attack vineyards resulting in very intensive pesticide treatments; approximately 20% of the phytochemicals sprayed in agriculture in France, measured in tons, are used to treat vineyards (Aubertot *et al.*, 2006). Moreover, this perennial crop hosts a large number of different pest species and grows in areas that are expected to experience climate change in the near future with important consequences for crop production and biodiversity (Hannah *et al.*, 2013). Reducing agrochemical use at the same time as maintaining yield and preserving biodiversity in those agroecosystems will therefore be a major applied challenge in the near future.

Our experiment used two common leafhopper (Hemiptera: Cicadellidae) species that infest vines: the green leafhopper *Empoasca vitis* (Gothe) and the Flavescence dorée leafhopper *Scaphoideus titanus* (Ball). These two leafhoppers can cause severe damage to grapevine. *Empoasca vitis* feeds by puncturing phloem vessels of the leaves leading to obstruction of the vessels and leaf necrosis, thereby resulting in a reduced photosynthetic rate and delayed fruit maturity (Chuche & Thiéry, 2014). *Scaphoideus titanus* is the only known vector of Flavescence dorée, a phytoplasma-borne disease, one of the most severe and damaging diseases in European vineyards; this disease causes major economic losses (Chuche & Thiéry, 2014). These two leafhopper species are found at the same time period on vines but usually occur at different phenological stages (adult and larva). Both species are mainly active at night (from 18.00 to 08.00 h) and stay on the leaves during the day (Lessio & Alma, 2004).

Several predatory species prey on grapevine insect pests (Sentenac, 2011). Among these, we selected three common predators of leafhoppers that have a major role in terms of top-down control in vineyards: the earwig *Forficula auricularia* L., the harvestman *Phalangium opilio* L. and the jumping spider *Salticus scenicus* (Clerck) (Sentenac, 2011; Hogg & Daane, 2013). We selected these species because they form typical assemblages found in vineyards and because they differ in their habitat domains and particularly in their traits related to hunting mode and daily activity (Schmitz, 2007; Sentenac, 2011). *Forficula auricularia* is an active and nocturnal predator (Suckling *et al.*, 2006); *P. opilio* is a nocturnal ambusher (Pinto-da-Rocha *et al.*, 2007); and *S. scenicus* is an active diurnal spider (Ubick *et al.*, 2005). All of these predators are known to hunt in the foliage where the two prey species occur.

Based on the various traits of both prey and predators used in this experiment, theory predicts a substitutive effect (linear averaging) in the multiple predator assemblage because of spatially and temporally complementary habitat domains (Schmitz, 2007). However, climatic warming is expected to affect the metabolism and behaviour of individuals. The outcomes of multiple predator effects in a warming context will be determined by the respective thermal tolerance and physiological demands of a given predatory species (Schmitz & Barton, 2014).

Experimental design

Predator assemblages were created using a substitutive design to give three single-species (low diversity) and one three-species (high diversity) treatments. All prey and predators were collected from local fields and were maintained in the laboratory for several days before the experiments. No food was made available to any predators for 72 h prior to the beginning of the experiment. Because the predators had differences in body mass, the number of individuals across species was standardized using allometric scaling of metabolic rate (*B*) to body mass (*M*) of $B = M^{3/4}$ (West *et al.*, 1997; Brown *et al.*, 2004). This standardization allows an examination of the effect of species richness independently of individual density of each species. The density of individuals used in the different treatments was consistent with the natural occurrence of these species in the field and represents the typical assemblages encountered in vineyards (Sentenac, 2011). Using allometric scaling of metabolic rate, we therefore used three *F. auricularia*, three *P. opilio* and six *S. scenicus* in the single-species treatments, whereas one *F. auricularia*, one *P. opilio* and two *S. scenicus* were used in the three-species treatment. In addition to the four predator treatments, we added a control treatment containing only prey.

Each experimental unit consisted of a cylinder of $15 \times 70\,\text{cm}^2$ mesocosm made of transparent plastic sheeting and with mesh on the top and side panels. One 2.5-month-old potted plant of *V. vinifera* with 8–10 leaves was placed in each mesocosm. In each mesocosm, 13 adults of *E. vitis* and 13 third-instar nymphs of *S. titanus* were introduced into the cages and allowed to settle for 8 h before introducing the predators. We selected adults of *E. vitis* and third-instar nymphs of *S. titanus* because this prey assemblage is representative of assemblages found in June. The experiment was performed in Conviron growth chambers (Controlled Environments Limited, Canada). Two types of mesocosms were prepared: ambient temperature (current June seasonal temperatures) and warmed by 3 °C above the current temperature, which is the predicted temperature increase in our area by 2100 (IPCC, 2007) (Table 1 provides the hourly variations in temperature, humidity and light for a 24-h period). The ambient treatment was based on a 10-year average of temperature found in June in our area (southwestern France).

Each combination of the five predator treatments at two temperatures was replicated three times for a total of 30 cages ($5 \times 2 \times 3 = 30$). Each appropriate predator assemblage was introduced into each mesocosm 8 h after prey introduction. At the end of the experiment, 72 hours after prey introduction, each mesocosm was exhaustively sampled and all living and dead predators and prey were recorded. This short time scale was chosen in accordance with Wilby *et al.* (2005) to isolate the complementarity of function from confounding effects of changes in prey and predator density. All the experiments were performed in the laboratory and did not involve any endangered or protected species.

Table 1 Hourly variation in temperature, humidity and light for a 24-h period for the two temperature treatments applied in climatic chambers

Time (h)	T_0 (°C)	T_1 (°C)	RH (%)	Fluor (μmol/m^2/s)
00.00–03.00	15	18	80	0
03.00–06.00	14	17	80	0
06.00–07.00	15	18	80	300
07.00–08.00	17	20	60	600
08.00–09.00	18	21	60	1000
09.00–10.00	19	22	60	1000
10.00–11.00	20	23	60	1000
11.00–12.00	21	24	60	1000
12.00–15.00	22	25	60	1000
15.00–17.00	23	26	60	1000
17.00–18.00	22	25	60	1000
18.00–19.00	21	24	60	600
19.00–20.00	20	23	60	600
20.00–22.00	18	21	60	300
22.00–23.00	17	20	80	0
23.00–00.00	16	19	80	0

T_0 represents the control treatment (which is based on a 10-year average of present temperatures found in our region during the month of June); T_1 represents an increase in temperature by 3 °C above T_0, which is the predicted temperature increase in our area by 2100 (IPCC, 2007). RH, relative humidity; Fluor, fluorescent lighting. These two variables did not differ between temperature treatments**.**

Prey selectivity

We computed a prey selectivity index (α_i) for each predator treatment in each temperature condition to examine a potential switch in prey preference between ambient and warmed temperatures. We calculated the α index in accordance with Chesson (1983) based on the number of prey recaptured at the end of the experiment using:

$$\alpha_i = \frac{r_i/p_i}{\sum_{i=1}^{m} r_i/p_i} \tag{1}$$

where r_i is the number of prey type *i* consumed by the predator, p_i is the number of prey type *i* at the beginning of the experiment and *m* is the number of prey species. We first computed the prey selectivity index for each individual predator treatment and then for the multiple predator treatment. When computed for a single species, this index can be interpreted as the preference of a given predatory species for a prey type relative to the preference for alternative prey. When computed for the multiple species treatment, this index can be interpreted as the preference of a given predator community for a prey type relative to the preference for alternative prey. These indices may range from 0 to 1, where 0 means total avoidance of the prey species, and 1 is total selection of the prey. An index value of 0.5 indicates that the predatory species does not have any preference for any prey. In this experiment, a low selectivity for a given species indicates a high preference for the other species because only two prey species were used.

Statistical analysis

We examined the effects of predator diversity and warming on the final leafhopper abundance using a two-way analysis of variance (ANOVA) (with an interaction term between the predator assemblages and the temperature effects) followed by Tukey's test whenever a significant difference was detected. A graphical validation procedure was applied to check for normality and homoscedasticity of the residuals and to ensure none of the assumptions were violated. We also calculated the expected multiple predator effect on leafhoppers for ambient and warmed temperature treatments by averaging the individual effects of a single predatory species on leafhopper abundance. The expected values were compared with their corresponding measured multiple predator effect using one-tailed, one-sample *t*-tests in accordance with Barton and Schmitz (2009). Kruskal–Wallis one-way ANOVA was used to analyze the effects of warming on prey selectivity for each predator treatment. In addition, we analyzed the effects of predator diversity and warming on the proportion of predators collected at the end of the experiment using a two-way ANOVA (with an interaction). The no predator treatment was not considered in this analysis and we used the proportion of predator collected at the end of the experiment because the total number of individuals introduced varied among treatments. This variable provides information about the level of cannibalism or intraguild predation in each treatment (Finke & Denno, 2005). Statistical analyses were performed using R, version 3.1.2 (R Development Core Team, 2014).

Results

Effects of predator diversity and warming on predation of E. vitis

Our analysis revealed that predator assemblages significantly altered *E. vitis* abundance ($F_{4,20} = 12.9$, $P < 0.01$), whereas the warming treatment did not ($F_{1,20} = 0$, $P = 1$) (Fig. 1). No effect of the interaction term ($F_{4,20} = 1.2$, $P = 0.33$) was revealed by the ANOVA (see Supporting information, Fig. S1). Tukey's test revealed significant differences between the no predator treatment and all the other assemblages (single and multiple predators); the abundance of *E. vitis* was always higher in the no predator treatment compared with treatments with predators (Fig. 1). The observed multiple predator effect in the ambient temperature treatment was not statistically different from expectations calculated on the average single predator effects ($t = -1$, d.f. = 2, $P = 0.42$) (Fig. 1). However, the observed multiple predator effect in the warming treatment tended to differ from the expected effect based on the average single predator effects ($t = -3.33$, d.f. = 2, $P = 0.07$) (Fig. 1). The observed abundance of *E. vitis* at the end of the experiment tended to be lower than expected based on the observed abundance measured in the single predator treatments (Fig. 1).

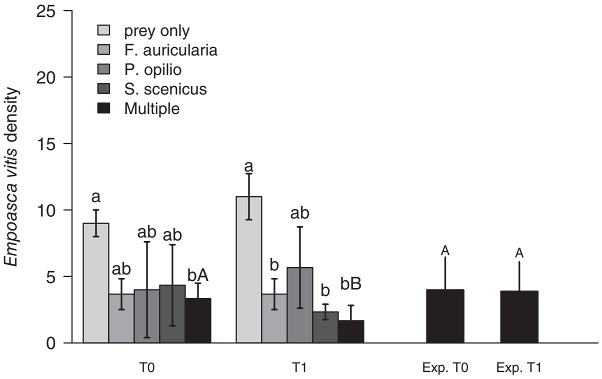

Figure 1 Effects of predator assemblage and experimental warming on *Empoasca vitis* density at the end of the experiment. Predator treatments are: (i) prey only (*E. vitis*); (ii) earwig (*Forficula auricularia*) and prey; (iii) harvestmen (*Phalangium opilio*) and prey; (iv) spiders (*Salticus scenicus*) and prey; and (v) all three predatory species and prey. T_0, ambient temperature; T_1, warmed by 3 °C above the ambient temperature. Values are the mean ± SD. Lowercase letters indicate significant differences between prey abundance within each temperature treatment (for details, see Statistical analysis). The two bars on the right are the expected multiple predator effect on leafhopper for both control and warming treatments by averaging the individual effects of single predatory species on leafhopper abundance. For each temperature treatment, uppercase letters indicate a significant difference between the expected and observed multiple predator effect based on a one-tailed, one-sample *t*-test.

Effects of predator diversity and warming on predation of S. titanus

Our analysis revealed that predator assemblages significantly altered *S. titanus* abundance ($F_{4,20} = 5.74$, $P < 0.01$), whereas the warming treatment did not ($F_{1,20} = 0.87$, $P = 0.36$) (Fig. 2). A significant effect of the interaction term ($F_{4,20} = 3.18$, $P = 0.03$) was detected by our analysis, indicating that the effects of various predator assemblages differed between the two temperature conditions (Fig. 2; see Supporting information, Fig. S1). Tukey's tests revealed no significant differences between predator assemblages in the ambient temperature treatment (Fig. 2). In the warmed conditions, we found significantly lower *S. titanus* in the multiple predator assemblage compared with the no predator or *F. auricularia* treatment (Fig. 2). The numbers of *S. titanus* in the *P. opilio* and *S. scenicus* treatments were at intermediate levels between the multiple predator and no predator treatments (Fig. 2). The observed multiple predator effect in the ambient temperature treatment was not statistically different from expectations calculated based on the average single predator effects (*t*-test, $t = 5$, d.f. = 2, $P = 0.98$) (Fig. 2). However, the observed multiple predator effect in the warming treatment was significantly different from the expected effect based on the average single predator effects (*t*-test, $t = -3.14$, d.f. = 2, $P = 0.04$) (Fig. 2). The observed abundance of *S. titanus* at the end of the experiment was significantly lower than

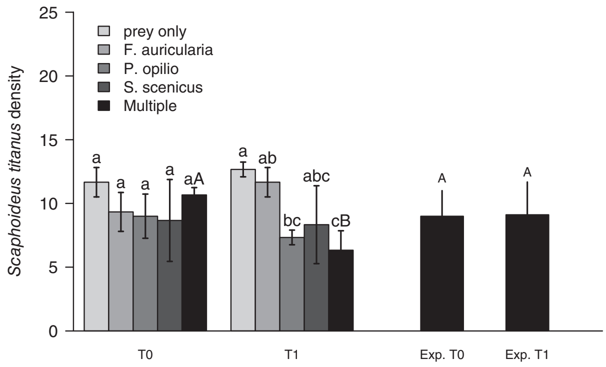

Figure 2 Effects of predator assemblage and experimental warming on *Scaphoideus titanus* density at the end of the experiment. Predator treatments are listed in Fig. 1: prey only (*Empoasca vitis*); earwig (*Forficula auricularia*) and prey; harvestmen (*Phalangium opilio*) and prey; spiders (*Salticus scenicus*) and prey; and all three predatory species and prey. T_0, ambient temperature; T_1, warmed by 3 °C above the ambient temperature. Values are the mean ± SD. Lowercase letters indicate significant differences between prey abundance within each temperature treatment (for details, see Statistical analysis). The two bars on the right are the expected multiple predator effect on leafhopper for both ambient temperature and warming treatments by averaging the individual effects of single predatory species on leafhopper abundance. For each temperature treatment, uppercase letters indicate a significant difference between the expected multiple predator effect and the observed multiple predator effect based on a one-tailed, one-sample *t*-test.

expected based on the observed abundance measured in the single predator treatments (Fig. 2).

Prey selectivity

Our results for prey selectivity indicated that the three predatory species generally have a preference for *E. vitis* over *S. titanus* (Prey selectivity value for *S. titanus* – ambient temperature: *P. opilio* = 0.30, *S. scenicus* = 0.32, *F. auricularia* = 0.27; warmed temperature: *P. opilio* = 0.44, *S. scenicus* = 0.28, *F. auricularia* = 0.10) (Fig. 3). However, our experiment revealed that warming modified prey selectivity. Our analysis of single predator treatments indicated the existence of a significant effect of warming on prey selectivity of *P. opilio* ($\chi^2 = 3.85$, d.f. = 1, $P = 0.04$) and *F. auricularia* ($\chi^2 = 3.97$, d.f. = 1, $P = 0.04$) and no significant effect of warming on prey selectivity of *S. scenicus* ($\chi^2 = 0.04$, d.f. = 1, $P = 0.82$) (Fig. 3). Warming increased the value of prey selectivity of *P. opilio* for *S. titanus*, changing from a clear preference for *E. vitis* (low prey selectivity value for *S. titanus*) to no preference between the two prey species (Fig. 3). Warming increased the preference of *F. auricularia* for *E. vitis* (Fig. 3). Our analysis of prey selectivity at the community level (multiple predatory species) revealed the existence of a significant effect of warming on prey selectivity of predators ($\chi^2 = 3.85$, d.f. = 1, $P = 0.04$) with a decreasing preference for *E. vitis* in a warming context (Fig. 3).

Proportion of predators collected at the end of the experiment

Our analyses revealed no difference in the proportion of predators collected at the end of the experiment between assemblages ($F_{3,16} = 1.33$, $P = 0.29$), warming treatments ($F_{1,16} = 0.17$, $P = 0.68$) or their interaction ($F_{3,16} = 0.38$, $P = 0.76$) (see Supporting information, Fig. S2).

Discussion

The present study demonstrated an interactive effect between predator diversity and warming on the predation of insect pests in vineyard. Experimental warming revealed complementarity between the predatory species in diverse assemblages because higher predation rates of both prey were found in the multiple predator treatment compared with that expected based on single predator treatments at the same temperature. This complementarity between species was not recorded in ambient temperature conditions. Our results therefore highlight the importance of maintaining diverse predator assemblages in a warming context if we are to increase the level of natural pest control services in agroecosystems.

The results of the present study indicate a shift from substitutive to complementarity effects among predatory species with experimental warming. This suggests modifications of interactions between predator species in diverse assemblages in such a context. Under ambient temperature conditions, the combined effects of different predatory species on the predation rates of both prey species were the linear average of the single predator effects. This outcome is in accordance with what was predicted based on theory related to multiple predator effects when predators have separate habitat domains and prey species have broad and overlapping habitat domains (Barton & Schmitz, 2009; Schmitz & Barton, 2014). However, under experimental warming, the multiple predatory species effect was higher than the linear average of the single predator effects resulting in higher predation rates. This result indicates the emergence of functional complementarity among predatory species under warming conditions. Other studies have reported that functional complementarity exists between species in diverse predator assemblages and it involved resource-niche partitioning and/or facilitation between predatory species (Straub & Snyder, 2008; Northfield *et al.*, 2010). To our knowledge, the present study is the first to demonstrate the emergence of such an effect with experimental warming.

Our analyses of prey selectivity provided evidence about the mechanisms that play a role in the emergence of functional complementarity. Our findings revealed a significant change in the feeding niche of two predatory species (*F. auricularia* and *P. opilio*) under temperature changes leading to a differentiation in the feeding niche at the community level. Potential mechanisms explaining a differentiation in the feeding niche might be a change in habitat domain of predator and/or prey species (Barton & Schmitz, 2009). Several studies have demonstrated that interspecific interactions and interspecific partitioning of foraging space are processes that may contribute to resource partitioning (Straub & Snyder, 2008; Northfield *et al.*, 2010). These processes may emerge with warming depending on predator and

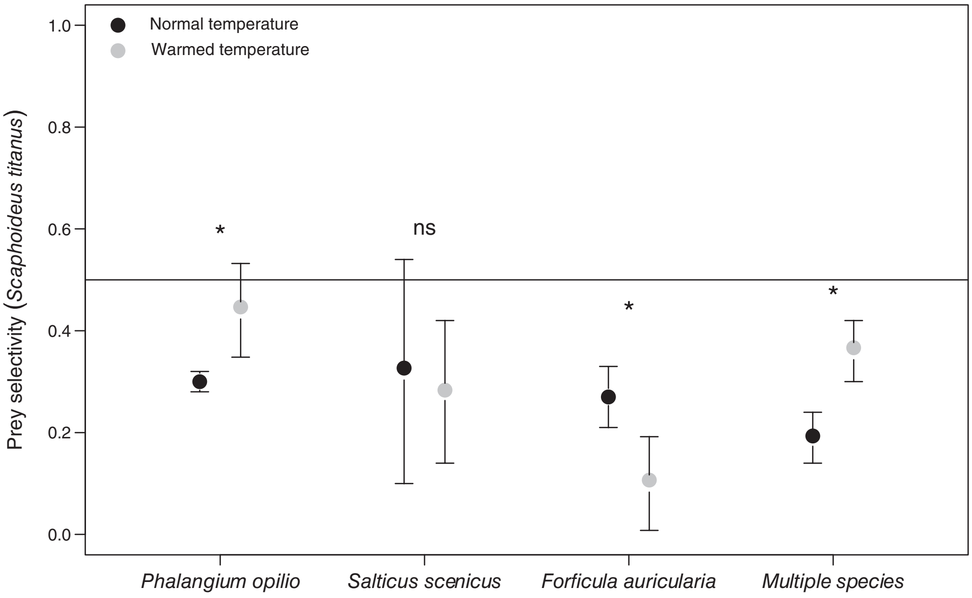

Figure 3 Prey selectivity index (α_i) calculated for each predator treatment (single species and multiple species treatments) and in each temperature condition (ambient temperature and warmed temperature). These indices range from 0 to 1, where 0 is total avoidance of the prey, and 1 is total selection of the prey. An index value of 0.5 indicates that the predatory species does not have any preference for any prey. A low selectivity for *Scaphoideus titanus* indicates a high preference for *Empoasca vitis* because two prey species (*E. vitis* and *S. titanus*) were used in this experiment. Values are the mean ± SD. *Significant differences in prey selectivity between ambient and warmed temperatures tested with a Kruskal–Wallis one-way analysis of variance.

prey behaviour, metabolism, or on their respective degree of thermal tolerance that may modify the spatio-temporal feeding niches of each species and generate separate habitat domains (Barton & Schmitz, 2009). Warming may also strengthen this effect because it increases the activity of ectothermic organisms and therefore increases the area searched and the number of prey and predators encountered (Lang *et al.*, 2012). Depending on prey mobility, actively roaming predators may experience more intense interspecific or intraspecific competition than their prey, which might increase the effects of resource use complementarity (Griffin *et al.*, 2008; Northfield *et al.*, 2010; Vucic-Pestic *et al.*, 2011). Intraguild predation and/or cannibalism have been reported for all the three predator species used in the present study (Polis, 1981; Pinto-da-Rocha *et al.*, 2007). However, our results revealed no effect of predator assemblage and warming treatment on the proportion of introduced individuals collected at the end of the experiment. This suggests that intraguild predation and/or cannibalism among predators were not involved in the observed effect.

Facilitation between predatory species is often reported in the literature as a mechanism that explains functional complementarity (Losey & Denno, 1998; Letourneau *et al.*, 2009). Theoretically, an increase in the activity of predators caused by warming may enhance synergistic effects because facilitation exists between species such as cooperative foraging or conflicted prey escape behaviour (Losey & Denno, 1999; Griffin *et al.*, 2013). Although several studies have demonstrated facilitation between predators, we do not have specific evidence from the present study, nor have we found any evidence in the literature related to the probability of the occurrence of such a mechanism in our study system. Therefore, we cannot exclude that such processes may also be involved in the observed pattern.

In a different study system, Barton and Schmitz (2009) found that warming transforms exploitative competition to an intraguild predation system with an overlap in the feeding-niche of two spider species. In their study, Barton and Schmitz (2009) showed that intraguild predation emerged because of a shift in the spatial habitat domain of one predatory species driven by its thermal tolerance. Although we used different biological systems and a different experimental approach, our respective studies highlight the high context dependency of the effects of warming on trophic interactions in arthropod communities. Further studies in different contexts and with different species are therefore needed if we are to understand the consequences of climate change on trophic interactions in ecosystems.

The present study also contributes to the ongoing debate related to how species diversity affects ecosystem functioning in agroecosystems in a global change context (Cardinale *et al.*, 2012). Our findings demonstrate that a positive relationship exists between diversity and ecosystem functioning in a warming context. Our work, together with the large body of work related to biodiversity and ecosystem functioning, highlights the importance of conserving species-rich assemblages of predators to buffer the effects of climatic warming (Wilmers & Getz, 2005). This is especially important in agroecosystems if we are to strengthen the reliance of agricultural production on ecosystem services and limit the negative effects of chemical pesticides on the environment. Moreover, the present study provides an empirical application of the theoretical framework proposed by Schmitz (2007) that can be used to understand how multiple predatory species affect shared prey species based on specific functional traits. Further experiments are now needed in real cropping systems to confirm this interactive effect of predator diversity and warming. Particularly, studying the long-term consequences of changes in temperature and predator biodiversity appears to be a major challenge that should be addressed in future studies.

From an applied perspective, the present study has important implications for grapevine pest and disease management in a climate change context. Among the two studied pest species, *S. titanus* is a major pest of grapevine because it is the vector of the Flavescence dorée disease, which is a serious threat to European viticulture. Currently, *S. titanus* is present up to the 45th degree of latitude in Europe, although it is progressively extending the northern border of its range (Reineke & Thiéry, 2016). With a potential increase of summer temperatures in the near future, this insect will certainly have the potential to become established in wine-growing regions north of the 46th degree of latitude. The present study therefore highlights the need to preserve predator biodiversity in vineyard landscapes, in addition to other management approaches, with the aim of limiting the spread of the insect vector and therefore the disease.

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Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference:
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Fig. S1. Interaction plots for analysis of variance examining (a) the effect of predator diversity and warming on *Empoasca vitis* abundance and (b) the effect of predator diversity and warming on *Scaphoideus titanus* abundance.

Fig. S2. Effects of predator assemblage and experimental warming on the proportion of predator collected at the end of the experiment. No statistical differences were found between treatments. Predator treatments comprise: earwig (*Forficula auricularia*), harvestmen (*Phalangium opilio*), spiders (*Salticus scenicus*) and all three predatory species together. T0, ambient temperature; T1, warmed by 3 °C above the ambient temperature.

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