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Effet de la température sur les interactions trophiques et intraguildes au sein d'un système plante-herbivore-ennemis naturels : modélisation et approches expérimentales

par
Arnaud Sentis

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Cette thèse intitulée :

Effet de la température sur les interactions trophiques et intraguildes au sein d'un système plante-herbivore-ennemis naturels : modélisation et approches expérimentales

présentée et soutenue à l'Université de Montréal par :
Arnaud Sentis

a été évaluée par un jury composé des personnes suivantes :
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Président-rapporteur

Jacques Brodeur, Ph.D., Université de Montréal
Directeur de recherche

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Jean-François Masson
Représentant du doyen de la faculté des études supérieures

Résumé

Il est maintenant reconnu que les changements climatiques ont des impacts importants sur l'ensemble des organismes vivants. Parmi les facteurs de ces changements, la température occupe une place prépondérante pour les organismes ectothermes car elle régule leur métabolisme. Toutefois, bien que les effets de la température sur les individus d'une espèce soient largement connus, les connaissances demeurent limitées quant aux conséquences sur les interactions trophiques. Dans ce contexte, notre étude s'intéresse aux effets de la température sur un système biologique composé d'une plante, le poivron *Capsicum annuum* L., d'un herbivore, le puceron *Myzus persicae* Sulzer (proie extraguilde), ainsi que de deux de ses ennemis naturels : la coccinelle maculée *Coleomegilla maculata lengi* Timberlake (prédateur intraguilde) et la cécidomyie prédatrice *Aphidoletes aphidimyza* Rondani (proie intraguilde). Dans ce but, nous avons opté pour une approche multiple comprenant : (1) la modélisation des interactions prédateur-proie et intraguilde (prédation entre deux compétiteurs d'espèces différentes qui exploitent une même ressource), (2) la réalisation d'expériences empiriques en laboratoire permettant de tester les prédictions des modèles et de caractériser l'effet de la température et de ses variations sur les composantes du système biologique étudié. Conformément aux prédictions d'un premier modèle, nous mettons en évidence que, lorsque la température augmente, *C. maculata* est plus efficace pour trouver et manipuler ses proies, ce qui augmente le taux de prédation. En revanche, à haute température son efficacité de recherche décroît, ce qui entraîne une diminution du taux de prédation. L'activité de prédation se limite donc à une fenêtre thermique en dehors de laquelle elle est réduite ou nulle. Par la suite, nous comparons un modèle linéaire et un modèle non-linéaire (saturant à haute densité de proies) afin de déterminer lequel de ces deux modèles décrit le mieux la réponse fonctionnelle d'un prédateur intraguilde, c'est-à-dire la relation entre le nombre de proies consommées et la densité de proies. Nos résultats expérimentaux démontrent que les prédictions du modèle non-linéaire correspondent bien aux observations empiriques, tandis que le modèle linéaire surestime largement le nombre de proies consommées et la fréquence des interactions intraguildes. Par la suite, nous dérivons le modèle non-linéaire afin d'y inclure l'effet de la température. Comme prédit par ce dernier modèle, la prédation intraguilde devient plus fréquente lorsque la température augmente mais diminue lorsqu'il y a davantage de proies extraguildes. Dans une dernière étude, nous soumettons le système biologique à des pics de température. Nos résultats démontrent que ces pics diminuent la fécondité des pucerons, l’accroissement de leurs populations, le poids des larves de coccinelles et le contrôle des pucerons par les coccinelles mais n’ont pas d’effets sur la plante et les relations plante-insecte. Le système biologique s’avère également plus résistant aux pics de température en présence de coccinelles qu’en leur absence. En conclusion, notre étude souligne l’importance de considérer la température dans les interactions trophiques puisqu’elle influence le comportement des organismes et la fréquence de leur interaction, ce qui se répercute au niveau des populations et des communautés.

Mots clés. Changements climatiques, température, interaction multitrophiques, modélisation, réponse fonctionnelle, prédation intraguilde, puceron vert du pêcher, prédateurs aphidiphages.

Abstract

There are several pieces of evidence that climate change significantly impact plants, herbivores, and predators. For ectotherms, temperature is the most important factor associated with these changes as it regulates their metabolism. Although the effects of temperature on individual organisms or populations have been well documented, our understanding about their consequences on trophic and guild interactions remains limited. In this context, we investigated the effects of temperature on complex interactions between a plant, the pepper *Capsicum annuum* L.; an herbivore, the aphid *Myzus persicae* Sulzer (extraguild prey); and two of its natural enemies, the ladybeetle *Coleomegilla maculata* lengi Timberlake (intraguild predator) and the predatory midge *Aphidoletes aphidimyza* Rondani (intraguild prey). We combined two approaches: (1) modeling predator–prey and intraguild (predation between two species that compete for the same resource) interactions, and (2) testing model predictions and characterizing the effects of temperature on components of our biological system through laboratory experiments. As predicted by the first model, we found that when temperature rises, *C. maculata* is more efficient at finding and handling prey, which increases predation rate. However, search rate decreases at high temperatures, leading to a reduction in predation. The predatory activity is therefore limited to a temperature window outside of which predation is reduced or absent. The next objective was to compare two models, one linear and one nonlinear, to determine which one best describes the functional response (the relationship between the number of prey consumed and prey density) of an intraguild predator. Results indicated that predictions of the nonlinear model (i.e., saturating at high prey densities) fit empirical observations well while the linear model greatly overestimates the number of prey consumed and the incidence of intraguild predation. Subsequently, we derived the nonlinear model to include the effect of temperature. As predicted by this model, we found that the incidence of intraguild predation increases with temperature but decreases when extraguild prey are more abundant. In a last experiment, we investigated the effects of temperature peaks on each component of our biological system. Results showed that temperature peaks reduce aphid fecundity and thereby population growth, decrease the weight of ladybeetle larvae, and decrease aphid control by ladybeetles, but have no effect on plants or plant–insect relationships. We also observed that the food chain is more resistant to temperature peaks when ladybeetles are included in the system than when they are absent. This suggests that ecosystems with predators exerting strong biotic control on prey population should be more resistant to climate change than ecosystem lacking them. In conclusion, our study highlights the importance of considering temperature in trophic and guild interactions since it influences the behavior of organisms as well as the frequency of interactions that affect population and community dynamics.

Key words. Climate change, temperature, multitrophic interactions, modeling, functional response, intraguild predation, green peach aphid, aphidophagous predators.

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AIC : critère d'information d'Akaïke

ANOVA : analyse de variance

CI : intervalle de confiance

***df* :** degré de liberté

EG : extraguilde

***et al.* :** et collègues

IG : intraguilde

IGP : prédation intraguilde

IPCC : « *intergovernmental panel on climate change* »

MTE : « *metabolic theory of ecology* »

***n* :** nombre de réplicas

***P* :** probabilité

SD : écart type

SE : erreur standard

X : moyenne

∅ : rayon

A ma famille de sang et de cœur,

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Plan de la thèse

Chapitre 1. Ce chapitre d'introduction vise à mettre en contexte l'ensemble de la thèse, à identifier la problématique à l'étude et à présenter les objectifs de la thèse.

Chapitre 2. Afin que le lecteur ait en main toutes les informations nécessaires pour une bonne compréhension de la thèse, ce chapitre présente le système biologique à l'étude ainsi qu'une revue de littérature des concepts et des connaissances sur lesquels s'appuie la présente thèse.

Chapitre 3. Ce chapitre décrit ma contribution et celles des co-auteurs aux différents articles scientifiques inclus dans la thèse.

Chapitre 4. Un premier article scientifique intitulé «Using functional response modeling to investigate the effect of temperature on predator feeding rate and energetic efficiency» présente un nouveau modèle de réponse fonctionnelle dépendant de la température ainsi que sa validation expérimentale.

Chapitre 5. Le deuxième article s'intitule «How functional response and system productivity modulate intraguild predation». Nous y développons et testons différents modèles afin de prédire l'intensité de la prédation intraguilde en fonction de la densité de proies extra- et intraguildes.

Chapitre 6. Le troisième article s'intitule «Effects of temperature and prey density on intraguild predation: combining modeling and experimental approaches». En se basant sur l'article précédent, nous développons, testons et validons un modèle qui prédit l'effet de la température et de la densité de proies extraguildes sur l'intensité de la prédation intraguilde.

Chapitre 7. Le dernier article s'intitule «Effects of extreme temperature fluctuations on a plant–herbivore–predator system». Il examine l'effet de la prédation, de la fréquence et de l'amplitude de pics de température (i.e. augmentation ou diminution brève de la température) sur les organismes étudiés et leurs interactions.

Chapitre 8. Ce dernier chapitre, la conclusion générale de la thèse, constitue une synthèse des résultats présentés et discute des implications théoriques et pratiques des résultats de notre étude.

Chapitre 1

Introduction générale

Depuis la révolution industrielle, l'activité humaine a entraîné une augmentation de la concentration atmosphérique des gaz à effet de serre de plus de 70 %, ce qui provoque actuellement des changements climatiques importants (IPCC 2007). Selon le quatrième rapport de l'*Intergovernmental Panel on Climate Change* (IPCC 2007), les émissions mondiales de gaz à effet de serre devraient s'accroître davantage d'ici 2030 et la température moyenne globale augmenterait alors d'environ 0,2°C par décennie. A l'échelle de la planète, les précipitations, le niveau des océans, les radiation ultraviolettes ainsi que les événements climatiques extrêmes augmenteraient aussi, mais il est difficile de prédire quelle sera l'ampleur de ces augmentations (Coviella & Trumble 1999; Parmesan 2006). L'ensemble de ces changements affecte la phénologie, l'abondance et la distribution d'un nombre important d'espèces de microorganismes, de plantes et d'animaux et, à plus long terme, la biodiversité et la stabilité des écosystèmes (Parmesan 2006). Néanmoins, parmi l'ensemble des facteurs associés aux changements climatiques, la température a le plus d'influence sur l'histoire de vie des organismes ectothermes (Parmesan 2006; Porter *et al.* 1991; Stacey 2003). La présente thèse se concentre donc principalement sur l'effet de la température et de ses variations sur les insectes et leurs interactions.

Une faible variation de température peut influencer l'activité métabolique des organismes (Brown *et al.* 2004), modifiant profondément leur comportement ainsi que leur taux de développement, leur fécondité et l'incidence de leur mortalité (Parmesan 2006; Porter *et al.* 1991; Vasseur & McCann 2005). Par conséquent, la température a un effet majeur sur la dynamique des populations de la majorité des organismes ectothermes tel que rapporté par un nombre important d'études (Brown *et al.* 2004; Dell *et al.* 2011; Englund *et al.* 2011; Petchey *et al.* 2010). Les effets des températures constantes sur les organismes sont largement connus mais, en revanche, ceux des variations de températures et des températures extrêmes le sont beaucoup moins alors que les climatologues prédisent qu'elles devraient augmenter en fréquence et en intensité dans les prochaines années (IPCC 2007).

De plus, nos connaissances sont limitées concernant l'effet de la température sur les interactions trophiques. Dans les communautés naturelles, chaque espèce interagit avec un grand nombre d'autres espèces. Il est donc essentiel de déterminer l'effet de la température et de ses variations sur les interactions trophiques afin de mieux comprendre et prédire l'effet des changements climatiques sur la dynamique des populations et le fonctionnement des écosystèmes (Tylianakis *et al.* 2008; Van der Putten *et al.* 2010). C'est un enjeu capital pour l'humanité car nous dépendons largement des écosystèmes pour notre alimentation et notre qualité de vie (Vitousek *et al.* 1997).

Dans cette thèse, nous avons choisi d'étudier deux types d'interactions trophiques, soit : prédateur-proie et intraguilde, c'est-à-dire la prédation entre deux compétiteurs d'espèces différentes qui exploitent une même ressource (Lucas *et al.* 1998; Polis *et al.* 1989). Ces interactions sont importantes et communes dans la plupart des communautés naturelles et anthropisées (Arim & Marquet 2004; Polis *et al.* 1989; Vance-Chalcraft *et al.* 2007) mais les effets de la température et de ses variations sur ces dernières restent peu connus. C'est pourquoi, dans la présente étude, nous désirons décrire et quantifier ces effets sur l'histoire de vie et les relations de prédation et de prédation intraguilde (IGP) chez les arthropodes. Afin d'étudier cette problématique, nous avons utilisé un système biologique qui inclut une plante, le poivron *Capsicum annuum* L. (Solanales : Solanaceae), un herbivore, le puceron vert du pêcher *Myzus persicae* Sulzer (Homoptera : Aphididae), ainsi que deux de ses ennemis naturels : la coccinelle maculée *Coleomegilla maculata lengi* Timberlake (Coleoptera : Coccinellidae) et la cécidomyie prédatrice *Aphidoletes aphidimyza* Rondani (Diptera : Cecidomyiidae). Dans un premier temps, nous avons développé une série de modèles afin de comprendre et prédire l'effet de la température sur les interactions prédateur-proie et intraguilde. La réalisation d'expériences en chambres de croissance nous a ensuite permis de manipuler les facteurs biotiques et abiotiques afin de quantifier leurs effets sur le système étudié et de tester les prédictions des modèles.

Les principaux objectifs de cette thèse sont les suivants : (1) développer, à l'aide du système biologique à l'étude, un modèle analytique afin de prédire l'effet de la température sur le comportement, le taux de prédation et l'efficacité énergétique d'un prédateur aphidiphage en fonction de la densité de ses proies, (2) développer, tester et valider un modèle analytique qui prédit le nombre de proies consommées par un prédateur intraguilde et l'intensité de la prédation intraguilde en fonction de la densité de proies, (3) inclure l'effet de la température dans le précédent modèle et tester les prédictions qui en découlent à l'aide de notre système biologique et (4) déterminer les effets de fluctuations extrêmes de température sur les organismes étudiés, leurs interactions et la dynamique du système biologique. Veuillez noter que des objectifs plus spécifiques et des hypothèses, lorsque requis, se retrouvent dans chacun des chapitres.

Chapitre 2

Revue de littérature

Ce chapitre comporte une brève revue de littérature des concepts et des connaissances sur lesquels s'appuient la présente thèse afin que le lecteur se familiarise avec les informations nécessaires à une bonne compréhension de la présente étude. Dans un premier temps, nous verrons comment la température influence les relations prédateur-proie de par son effet sur le métabolisme, le comportement et la réponse fonctionnelle des prédateurs ectothermes. Ensuite, le concept de prédation intraguilde, son importance en écologie des populations et les différents modèles qui en découlent sont présentés. Une autre section détaille les effets directs et indirects des températures extrêmes sur les systèmes multitrophiques. Pour terminer, nous décrivons le modèle biologique utilisé.

1. Effet de la température sur les relations prédateur-proie

La température, facteur abiotique aux amplitudes très variables en nature, a une influence considérable sur l'ensemble des organismes, particulièrement les ectothermes. Elle régule directement l'activité métabolique de ces derniers (Brown *et al.* 2004) et tout ce qui en découle : locomotion, alimentation, développement, reproduction, survie (Bale *et al.* 2002; Harrington *et al.* 2001). Par conséquent, un changement de température peut modifier les interactions prédateur-proie de multiples façons puisque les protagonistes peuvent répondre différemment à une variation de température. On peut alors observer des modifications de la physiologie et du développement des prédateurs et des proies (Vucic-Pestic *et al.* 2011), de la capacité de localisation ou du taux de rencontre des proies (Elliott *et al.* 2000), de la réponse numérique des prédateurs (Vasseur & McCann 2005) et de la niche temporelle au cours de laquelle les organismes sont actifs (Bale *et al.* 2002; Cammell & Knight 1992). Dans la suite du texte, nous aborderons principalement l'effet de la température sur le métabolisme, le comportement et la réponse fonctionnelle des prédateurs ectothermes car ceci constitue le cœur de notre travail.

1.1. Effet de la température sur le métabolisme des organismes

Le métabolisme désigne l'ensemble des réactions chimiques par lesquelles les cellules d'un organisme produisent et utilisent l'énergie. La température influence l'activité enzymatique des réactions biochimiques du métabolisme (Brown *et al.* 2004). Selon la théorie du *Metabolic Theory of Ecology* (MTE), le taux métabolique (I) de la grande majorité des organismes a la même dépendance à la température et se représente par l'équation suivante (Brown *et al.* 2004) :

$$I = i_0 M^{b_i} e^{-E_i / kT} \tag{1}$$

Avec i_0 une constante, b_i un exposant allométrique (0.75), E_i l'énergie d'activation du métabolisme, M la masse de l'organisme, k la constante de Boltzmann's (8.62×10^{-5} eV K^{-1}) et T la température en Kelvin.

Selon l'équation 1, le taux métabolique des organismes augmente exponentiellement avec la température. Cette relation a été validée pour la majorité des groupes d'organismes, depuis les eucaryotes unicellulaires jusqu'aux plantes et vertébrés (Brown *et al.* 2004). Néanmoins, certaines exceptions ont aussi été rapportées et cette relation n'est pas valide pour des températures élevées car le taux des réactions métaboliques fléchit aux températures supérieures à 40°C en raison de la dénaturation des enzymes impliquées (Davis *et al.* 2006; Gillooly *et al.* 2001). Comme tous les modèles, celui du MTE a donc ses limites. Toutefois, il s'avère fort important en écologie théorique puisqu'il permet de jeter les bases de l'effet de la température sur le métabolisme des organismes.

1.2. Effet de la température sur le comportement des prédateurs

Les comportements de prédation et d'alimentation des prédateurs dépendent largement de leur métabolisme : plus leur métabolisme est rapide, plus ils sont actifs et consomment de proies (Brown *et al.* 2004). Puisque le métabolisme des organismes augmente exponentiellement avec la température (Brown *et al.* 2004), les effets majeurs d'une élévation de température sont l'augmentation des taux d'activité et de prédation (Dixon *et al.* 2005; Elliott *et al.* 2000; Xia *et al.* 1999; Xia *et al.* 2003). Par exemple, chez les parasitoïdes, la vitesse de marche et le taux de parasitisme augmentent avec la température (Bourchier & Smith 1996). De même, chez des punaises du genre *Orius*, ou des coccinelles, la consommation quotidienne de proies s'accroît avec la température (Cocuzza *et al.* 1997; Ferran & Larroque 1979). Néanmoins, dans certains cas, on observe une diminution de l'activité de prédation lorsque les températures sont très élevées (Englund *et al.* 2011). L'effet de la température sur le comportement des prédateurs semble donc être spécifique à l'espèce ou dépendre de la fenêtre de températures testées mais, à ce jour, aucun consensus n'a émergé à ce sujet. Puisque le taux de prédation est un élément clé de la dynamique prédateur-proie et contribue largement à la dynamique des populations de proies et de prédateurs (McCann *et al.* 1998; Vasseur & McCann 2005), il est essentiel de développer des modèles et des approches expérimentales qui permettent de mieux comprendre l'effet de la température sur le taux de prédation des prédateurs.

1.3. Effet de la température sur la réponse fonctionnelle des prédateurs

La réponse fonctionnelle d'un prédateur se définit par la relation entre le nombre de proies consommées et le nombre de proies présentes (Holling 1959). C'est un concept important en écologie car il détermine la quantité d'énergie disponible pour le développement et la reproduction des prédateurs, ce qui se répercute sur la dynamique des populations de prédateurs et de leurs proies (McCann *et al.* 1998; Vasseur & McCann 2005). Il existe plusieurs types de réponse fonctionnelle dont les plus communs sont le type I (relation positive linéaire), le type II (courbe logarithmique) et le type III (courbe sigmoïdale) (Fig. 1) (Holling 1959). Le type I, moins abondant en nature, se retrouve chez les prédateurs passifs comme les araignées tisseuses de toiles ou les mollusques (Holling 1959). Le type III est souvent associé aux prédateurs vertébrés comme les oiseaux ou les mammifères qui ont la faculté d'apprendre à chercher leur proie ou à permuter d'espèce de proie en fonction de la densité de ces dernières (Holling 1959). Ces deux mécanismes expliqueraient pourquoi la proportion de proies consommées augmente à densité intermédiaire de proie (Fig. 1). Néanmoins, la plupart des expériences empiriques démontrent que la majorité des prédateurs, en particulier les invertébrés, ont une réponse fonctionnelle de type II (Jeschke *et al.* 2002), c'est-à-dire que la consommation de proies augmente avec la densité de celles-ci pour atteindre un plateau. Selon Holling (1959), la réponse fonctionnelle d'un prédateur dépend de deux facteurs : le temps de manipulation (le temps requis pour attaquer, tuer et consommer une proie) et l'efficacité de recherche des proies (le nombre de proies détectées par unité de temps). De nombreux facteurs comme la taille relative des proies et leur distribution, la présence d'autres prédateurs, la complexité de l'habitat et la température peuvent influencer le temps de manipulation et/ou l'efficacité de recherche des prédateurs et, par conséquent, modifier leur réponse fonctionnelle (Englund *et al.* 2011; Mack *et al.* 1981; Messina & Hanks 1998; Skalski & Gilliam 2001; Xia *et al.* 2003). De manière générale, lorsque la température augmente, le métabolisme des prédateurs accélère et ils sont donc plus efficaces pour trouver et manipuler leurs proies, ce qui accroît le nombre de proies consommées par unité de temps (Englund *et al.* 2011; Mack & Smilowitz 1982). Néanmoins, aux températures minimales et maximales, l'activité de prédation est réduite ou nulle car les prédateurs sont inactifs (Englund *et al.* 2011; Mack *et al.* 1981; Mack & Smilowitz 1982). Par conséquent, des variations de température peuvent avoir des conséquences importantes sur la réponse fonctionnelle des prédateurs et donc sur les interactions prédateur-proie.

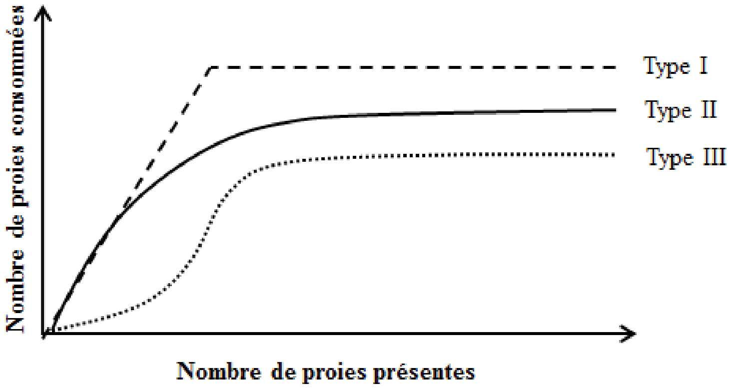

Fig. 1. Représentation schématique des trois principaux types de réponse fonctionnelle (i.e. relation entre le nombre de proies présentes et le nombres de proies consommées par un prédateur) : soit le type I (relation positive linéaire), le type II (courbe logarithmique) et le type III (courbe sigmoïdale) (Holling 1959).

1.4. Modélisation de la réponse fonctionnelle d'un prédateur

À ce jour, plus d'une centaine de modèles de réponse fonctionnelle ont été développés (Jeschke *et al.* 2002) mais le modèle de Holling (1959), aussi appelé l'équation du disque, reste le plus utilisé certainement pour sa simplicité mathématique et la facilité d'interprétation de ses paramètres (Jeschke *et al.* 2002). Cette équation représente la réponse fonctionnelle de type II et se définit par:

$$N_e = \frac{a \times N_0}{a \times Th \times N_0 + 1} \tag{2}$$

Avec N_e, le nombre de proies consommées par unité de temps; N_0, l'abondance des proies; Th, le temps de manipulation d'une proie (jour proie^{-1}) et a, l'efficacité de recherche des proies (m^2 jour^{-1}).

Bien que la température ait un effet important sur la réponse fonctionnelle des prédateurs, très peu de modèles en tiennent compte. Mack *et al.* (1981) et Flinn (1991) ont développé des modèles dans lesquels le temps de manipulation et l'efficacité de recherche sont fonction de la température. Néanmoins, leurs modèles manquent de réalisme et comportent de multiples paramètres qui n'ont pas toujours d'interprétation biologique (Flinn 1991). Par conséquent, ces modèles sont très peu utilisés et n'ont permis qu'une relative avancée théorique.

2. Effet de la température sur la prédation intraguilde

La prédation intraguilde (IGP) fait référence à la prédation entre deux compétiteurs d'espèces différentes qui exploitent une même ressource (Lucas *et al.* 1998; Polis *et al.* 1989) (Fig. 2). Cette interaction, commune dans la majorité des écosystèmes (Arim & Marquet 2004), a suscité depuis une vingtaine d'années un intérêt grandissant chez les scientifiques car elle peut influencer la structure et la stabilité des communautés naturelles et, d'un point de vue appliqué, l'efficacité du contrôle biologique des ravageurs agricoles et forestiers (Arim & Marquet 2004; Finke & Snyder 2010; Polis *et al.* 1989; Rosenheim 1998; Straub *et al.* 2008; Vance-Chalcraft *et al.* 2007) et la survie des espèces menacées (Müller & Brodeur 2002).

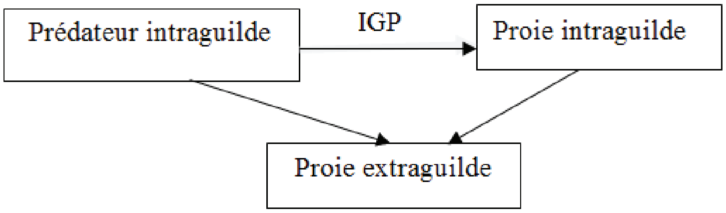

Fig. 2. Représentation schématique de la prédation intraguilde. Les flèches indiquent le sens de la prédation. IGP est l'acronyme de "Intraguild predation", soit la prédation intraguilde. Notez que, dans certains cas, il est possible que la proie intraguilde attaque, tue et/ou consomme le prédateur intraguilde. La prédation intraguilde est alors dite « symétrique » par opposition avec la prédation intraguilde « asymétrique » où la proie intraguilde est toujours la victime.

2.1. Facteurs qui influencent la prédation intraguilde

De nombreux facteurs tels que la taille relative des protagonistes, leur mobilité, leur spécificité alimentaire, leur moyen d'attaque et de défense peuvent influencer l'issue de l'interaction entre deux prédateurs (Hindayana *et al.* 2001; Lucas 2005). Dans la suite du texte, nous nous sommes essentiellement concentrés sur les deux facteurs qui ont été étudiés dans cette thèse : la densité de proies extraguildes et la température.

L'augmentation du nombre de proies extraguildes diminue généralement la probabilité de rencontre des prédateurs et, par conséquence, la fréquence des interactions intraguildes (revue par Lucas & Rosenheim 2011). Cette diminution est d'autant plus marquée lorsqu'attaquer la proie intraguilde représente un risque pour le prédateur intraguilde (Lucas 2005). En revanche, lorsqu'il est plus avantageux de consommer la proie intraguilde que la proie extraguilde, cet effet est atténué car le prédateur intraguilde cherche activement la proie intraguilde. Lucas (2005) a identifié trois types d'IGP qui correspondent à ce dernier scénario: (1) IGP nutritionnelle en raison de gains nutritionnels importants associés à la consommation de la proie intraguilde, (2) IGP compétitive car consommer la proie intraguilde élimine un compétiteur potentiel, et (3) IGP protective si consommer la proie intraguilde élimine un prédateur potentiel quand l'IGP est symétrique (lire Lucas 2005 pour plus de détails concernant les différents types de prédation intraguilde et pour des exemples concrets). L'effet de la densité des proies extraguildes sur la fréquence des interactions intraguildes varie donc en fonction du bénéfice lié à la consommation de la proie intraguilde par le prédateur intraguilde mais aussi du comportement des prédateurs et des proies, de la complexité de l'habitat et de la réponse numérique (c'est-à-dire l'augmentation du nombre de prédateurs en fonction de l'abondance des proies) des prédateurs (Chacón & Heimpel 2010; Finke & Denno 2002; 2006; Lucas 2005; Rosenheim & Corbett 2003; Schmitz 2007; Vucic-Pestic *et al.* 2011). De plus, à long terme, la densité des proies extraguildes, souvent reliée à la productivité du milieu dans les modèles théoriques, a un effet important sur la stabilité et la persistance des communautés intraguildes (voir section suivante).

Bien que la prédation intraguilde et certains facteurs qui la modulent soient relativement bien connus, les effets de la température sur cette interaction n'ont jamais été étudiés. Tel que mentionné ci-dessus, les études basées sur de simples systèmes prédateur-proie ont rapporté qu'un accroissement de la température entraîne une augmentation du métabolisme des prédateurs, de l'activité de recherche des proies et, par conséquent, du taux de rencontre avec les proies et du taux de prédation (Englund *et al.* 2011; Vasseur & McCann 2005; Vucic-Pestic *et al.* 2011; Zamani *et al.* 2006). Etant donné que la réponse du métabolisme à la température est similaire pour la plupart des prédateurs ectothermes (Brown *et al.* 2004), on peut s'attendre à ce que l'effet de la température soit analogue pour les interactions entre prédateurs. La fréquence des interactions intraguildes augmenterait alors avec la température. Néanmoins, cette hypothèse se doit d'être testée empiriquement.

2.2. Modélisation des interactions intraguildes

Depuis la publication d'une théorie générale concernant l'IGP (Holt & Polis 1997), un grand nombre de modèles ont été développés pour évaluer l'importance et la prévalence de celle-ci dans diverses communautés naturelles (Borer *et al.* 2003; Borer 2006; Borer *et al.* 2007; Diehl & Feissel 2000; Mylius *et al.* 2001). Selon ces modèles, l'IGP serait une interaction peu commune en nature puisque la coexistence entre les différents protagonistes s'avère possible seulement sous certaines conditions : (1) le système doit être relativement stable car des fluctuations trop importantes des effectifs entrainent la disparition d'une des espèces engagée dans cette interaction, (2) la proie intraguilde doit être plus performante que le prédateur intraguilde pour exploiter la proie extraguilde sinon le prédateur extraguilde élimine la proie intraguilde par compétition (niche exclusion) et prédation et (3) la productivité du milieu estimée par la densité de proies extraguildes doit être intermédiaire : à faible productivité, seule la proie intraguilde persiste car elle exploite mieux la proie extraguilde que le prédateur intraguilde (cf point 2) et, à haute productivité, la réponse numérique des prédateurs intraguildes est amplifiée ce qui contribue à éliminer la proie intraguilde par une intensification de la compétition et de la prédation (Borer *et al.* 2003; Borer *et al.* 2007; Diehl & Feissel 2000; Holt & Polis 1997; Mylius *et al.* 2001). Cependant, contrairement à la théorie, la majorité des études expérimentales en laboratoire et en nature ont observé que la coexistence peut être possible même en conditions de haute productivité (Amarasekare 2000; Amarasekare 2007; 2008; Borer *et al.* 2003; Brodeur *et al.* 2002; Lawler & Morin 1993; Lucas & Rosenheim 2011; Morin 1999). Une des explications proposées est qu'un grand nombre de modèles théoriques utilisent une réponse fonctionnelle de type I (Borer *et al.* 2003; Borer *et al.* 2007; Briggs & Borer 2005; Diehl & Feissel 2000; Hall 2011; Holt & Polis 1997) alors que ses prédictions sont peu réalistes, en particulier à haute densité de proies (Abrams & Fung 2010). Ainsi, des ajustements dans le type de la réponse fonctionnelle utilisée ont permis de réconcilier théorie et observations empiriques (Abrams & Fung 2010; McCann & Hastings 1997; McCann *et al.* 1998). Il est donc important d'évaluer la forme de la réponse fonctionnelle d'un prédateur intraguilde afin de mieux comprendre l'impact des interactions intraguildes sur la stabilité et la persistance des communautés à différents niveaux de productivité. Cependant, à notre connaissance, aucune étude expérimentale n'a été réalisée dans ce but.

3. Effet des températures extrêmes sur les populations d'insectes

Selon le quatrième rapport de l'IPCC (2007), l'augmentation des températures causée par les changements climatiques ne sera pas constante mais plutôt caractérisée par des fluctuations importantes et par une augmentation de la fréquence et de l'intensité des évènements climatiques extrêmes, une vague de chaleur intense par exemple. Jusqu'à présent la majorité des études concernant les changements climatiques se sont concentrées sur l'effet d'une augmentation moyenne de la température (Bale *et al.* 2002; Harrington *et al.* 1999; Parmesan & Yohe 2003), négligeant d'autant l'effet des températures extrêmes sur les écosystèmes et l'entomofaune (Smith 2011). Les températures extrêmes peuvent affecter les organismes directement et/ou indirectement par modification des interactions trophiques (Bannerman *et al.* 2011; Ciais *et al.* 2005; Smith 2011). Il est donc important de considérer ces deux aspects (Smith 2011).

3.1 Effets directs sur le développement, la survie et la fécondité des insectes

De manière générale, une légère augmentation de la température conduit à un accroissement de l'activité, du développement, de la reproduction et, dans certains cas, du nombre de générations par année (Asin & Pons 2001; Ayres & Lombardero 2000; Bayhan *et al.* 2005; Harrington *et al.* 2001; Holopainen & Kainulainen 2004; Porter *et al.* 1991). En revanche, les températures extrêmes, c'est-à-dire supérieures à 30°C pour les espèces des climats tempérés, peuvent avoir des effets négatifs sur la biologie des insectes, réduisant d'autant le taux intrinsèque d'accroissement de leurs populations (Davis *et al.* 2006; Mironidis & Savopoulou-Soultani 2008; Morgan *et al.* 2007; Wang & Tsai 2007; Yocum *et al.* 1991). Par exemple, Davis *et al.* (2006) ont observé que de faibles fluctuations de température augmentent l'aptitude phénotypique du puceron *M. persicae* mais, quand ces fluctuations excédent le seuil limite de température, la valeur adaptative du puceron diminue et sa population décline et peut disparaître. Ces effets sont généralement causés par la dénaturation de certaines protéines, l'inactivation d'enzymes et par des dérèglements du fonctionnement de membranes plasmiques (Davis *et al.* 2006; Mironidis & Savopoulou-Soultani 2008). Néanmoins, les insectes sont capables de supporter l'exposition à des pointes de températures élevées pourvu qu'elles soient séparées par une période de répit à température favorable (Davis *et al.* 2006; Mironidis & Savopoulou-Soultani 2008). L'ensemble de ces résultats suggèrent que la fréquence et l'amplitude des pics de température sont les deux principaux facteurs qui déterminent l'impact des températures extrêmes sur les insectes. Néanmoins, davantage d'expériences sont nécessaires pour le confirmer.

3.1 Effets indirects par les prédateurs et la plante ("*Top-down*" vs "*Bottom-up*")

La réponse de chaque espèce aux changements climatiques ne se déroule pas en vase clos mais dépend aussi des interactions avec les autres espèces (Tylianakis *et al.* 2008; Van der Putten *et al.* 2010). Il est donc essentiel de tenir compte de ces interactions pour prédire la distribution et l'abondance des insectes en réponse aux changements climatiques (Stenseth *et al.* 2002; Tylianakis *et al.* 2008; Van der Putten *et al.* 2010). Néanmoins, la majorité des études se sont concentrées sur un seul niveau trophique et on connait peu les effets de la température et de ses extrêmes sur les réseaux trophiques (Ciais *et al.* 2005; De Boeck *et al.* 2010; Gillespie *et al.* 2012).

La température peut affecter indirectement les populations d'herbivores et de prédateurs par les plantes (effet "*bottom-up*") (Barton *et al.* 2009; Barton 2011). En général, la survie, le développement, la reproduction et la taille des herbivores augmentent avec la qualité des plantes, ce qui se répercute sur les performances du prédateur (Barbosa *et al.* 1982; Francis *et al.* 2000; Greenblatt *et al.* 1982; Kagata *et al.* 2005). En revanche, lorsque les plantes sont de moindre qualité, le temps de développement des herbivores s'allonge, ce qui augmente la durée d'exposition aux ennemis naturels (Price *et al.* 1980; Stiling *et al.* 1999; Zvereva & Rank 2003). Plusieurs autres études démontrent aussi un effet de la qualité des plantes sur les niveaux trophiques supérieurs (Chen *et al.* 2005; Francis *et al.* 2000; Francis *et al.* 2001; Mayntz 2001). Étant donné que la température peut modifier la qualité nutritive des plantes (Bale *et al.* 2002), alors les températures extrêmes, par des effets de cascade, pourraient avoir des impacts importants sur la dynamique des populations d'herbivores et de prédateurs.

Un autre facteur peu connu est l'effet des ennemis naturels sur la dynamique des populations d'herbivores exposées à des températures fluctuantes et/ou extrêmes (effet "*top-down*"). La majorité des études, qui ont été réalisées à des températures constantes, démontrent que le taux de prédation augmente généralement avec la température (Englund *et al.* 2011; Mack & Smilowitz 1982; Xia *et al.* 2003; Zamani *et al.* 2007). Néanmoins, les températures extrêmes sont susceptibles d'affecter les prédateurs (Pörtner & Farrell 2008; Roux *et al.* 2010) et donc de diminuer la pression de prédation (Englund *et al.* 2011). Puisque toute modification des interactions prédateur-proie peut avoir des conséquences importantes sur la dynamique des populations de proies et de prédateurs, il est donc important de déterminer l'effet des températures extrêmes sur les interactions "*top-down*".

4. Système biologique étudié

Nous avons utilisé un système biologique qui inclut une plante, le poivron *Capsicum annuum* L. (Solanales : Solanaceae), un herbivore, le puceron vert du pêcher *Myzus persicae* Sulzer (Homoptera : Aphididae), ainsi que deux de ses ennemis naturels : la coccinelle maculée *Coleomegilla maculata lengi* Timberlake (Coleoptera : Coccinellidae) et la cécidomyie prédatrice *Aphidoletes aphidimyza* Rondani (Diptera : Cecidomyiidae). Notre choix pour ce système biologique a été motivé par le fait que *M. persicae* est un ravageur important des cultures de poivron et que *C. maculata* et *A. aphidimyza* sont utilisés en lutte biologique et sont souvent présents et abondants en milieu naturel et agricole.

4.1 Le poivron

Le poivron, originaire d'Amérique centrale et d'Amérique du Sud, fait partie de la famille des Solanacées. Au Canada, les principales provinces productrices du poivron sous serres sont l'Ontario, la Colombie-Britannique et l'Alberta, qui regroupent plus de 90 % de la production nationale (Agriculture et Agroalimentaire Canada 2006). En serre, le poivron est cultivé par la méthode hydroponique avec un régime informatisé de température, d'éclairage, d'apport en nutriments et d'humidité. La température de la serre est rigoureusement contrôlée et se situe entre 21 et 26°C selon la phénologie de la plante et le cultivar (Agriculture et Agroalimentaire Canada 2006). L'humidité doit être comprise entre 60 et 80 %, le pH optimal du sol est 5,8 et les concentrations de nutriments et de CO_2 sont aussi modifiées selon le stade de développement et le cultivar (Agriculture et Agroalimentaire Canada 2006).

Les maladies les plus fréquentes et les plus dommageables pour le poivron sont la pourriture fusarienne de la tige et des fruits, la pourriture grise (*Botrytis*), la pourriture pythienne des racines et, depuis peu, le blanc (Agriculture et Agroalimentaire Canada 2006). Les virus peuvent aussi causer de lourdes pertes de récoltes au niveau des exploitations serricoles. Les arthropodes les plus nuisibles sont les tétranyques, les pucerons, les aleurodes, les mouches sciarides, la fausse-arpenteuse du chou *Trichoplusia ni* Hübner (Lepidoptera : noctuidae) (en Colombie-Britannique), la pyrale du maïs *Ostrinia nubilalis* Hübner (Lepidoptera : Pyralidae) (en Ontario) et les thrips

(Agriculture et Agroalimentaire Canada 2006). Les principaux pucerons nuisibles sont le puceron vert du pêcher (*M. persicae*), le puceron du melon (*Aphis gossypii* Glover), le puceron de la pomme de terre (*Macrosiphum euphorbiae* Thomas) et le puceron de la digitale (*Aulacorthum solani* Kaltenbach) (Agriculture et Agroalimentaire Canada 2006).

4.1 Le puceron

Les pucerons forment un groupe très important d'insectes (Malais & Ravensberg 1993) avec plus de 4000 espèces dans le monde (Stadler & Dixon 2005). Ils mesurent de 1 à 10 mm et se nourrissent de la sève élaborée des plantes, ce qui peut provoquer le flétrissement et l'enroulement des feuilles, provoquant des dégâts importants aux cultures dans les régions tempérées (Dixon 1985). Lorsque les conditions sont favorables, ils se reproduisent par parthénogenèse, si bien que leurs effectifs deviennent rapidement très élevés (Stadler & Dixon 2005). De plus, ils rejettent du miellat, qui est colonisé par un champignon noir, appelé la fumagine (Stadler & Dixon 2005). La présence de ce champignon à la surface des feuilles réduit la pénétration de la lumière et diminue la photosynthèse et, par conséquent, le rendement et la qualité des fruits. De plus, les pucerons sont d'importants vecteurs de virus (Blackman & Eastop 2000). Ils peuvent donc induire des dommages économiques importants pour l'agriculture.

Les pucerons sont exploités par de nombreux prédateurs spécialistes ou généralistes tels que les coccinelles, les chrysopes et les larves de quelques espèces de diptères (Dixon 1998). En cas d'attaque, les pucerons peuvent émettre des phéromones d'alarme, ruer, sauter ou chuter de la plante hôte, s'enfuir en se déplaçant sur la plante (Francke *et al.* 2008). La nature, la fréquence et l'efficacité de ces moyens défensifs varient en fonction de l'espèce de puceron, de la plante hôte, de l'espèce et de la taille relative du prédateur et des conditions écologiques (Losey & Denno 1998).

Myzus persicae

Le puceron vert du pêcher, *M. persicae*, est une espèce très polyphage, qui utilise le pêcher comme hôte primaire mais s'attaque à des hôtes secondaires de plus de 40 familles de plantes (Blackman & Eastop 2000; Emden *et al.* 1969). Il mesure de 1,2 à 2,1 mm à l'état adulte et sa couleur varie du vert blanchâtre au noir, en passant par le jaune-vert, le vert, le vert-gris et le rose ou le rouge (Blackman & Eastop 2000). Il effectue quatre stades larvaires avant d'atteindre le stade adulte. Le temps développement varie de 9 à 12 jours, selon la température et la qualité de la plante-hôte (Emden *et al.* 1969). Du point de vue économique, il est un ravageur important des cultures comme la tomate, la pomme de terre et le poivron. De plus, il est un important vecteur de plus de 100 de virus (Kennedy *et al.* 1962). Son importance économique est donc considérable.

4.2 La coccinelle maculée

Coleomegilla maculata se retrouve essentiellement en Amérique du Nord (Gordon 1985), dans un grand nombre de cultures comme la pomme de terre, le maïs, la luzerne, la pomme, le pois, le poivron, la tomate et l'asperge (Coderre & Tourneur 1988; Gordon 1985; Hodek & Honěk 1996).

La coccinelle maculée a un développement holométabole avec quatre (parfois cinq) stades larvaires qui durent 15,2 jours à 26,7°C (2,7 jours pour le stade I, 2,9 jours pour le stade II, 4 jours pour le stade III et 5,6 jours pour le stade IV) (Warren & Tadic 1967). Le seuil thermique d'activité est de 14,4°C et la température optimale est de 25°C (Mack & Smilowitz 1982). En automne les adultes migrent vers les sites d’hibernation où ils forment des agrégations de plusieurs centaines d’individus. Au printemps les adultes quittent ces sites à la recherche de leurs lieux d’alimentation et de reproduction (Hodek & Honěk 1996).

Les larves et les adultes de *C. maculata* sont tous deux des prédateurs très polyphages (Hodek & Honěk 1996). Ils se nourrissent de nombreuses espèces de pucerons, de pyrale du maïs, de larves du doryphore de la pomme de terre, de pollen, d'œufs et de larves d'autres espèces de coccinelle (Gordon 1985; Hodek & Honěk 1996; Mack & Smilowitz 1982). De plus, on observe fréquemment des cas de cannibalisme alors que les larves qui viennent de naître mangent les œufs qui ne sont pas encore éclos (Warren & Tadic 1967). Le cannibalisme est aussi favorisé par le fait que les œufs sont pondus en groupe.

En général, les coccinelles aphidiphages n'ont pas beaucoup de prédateurs parmi les vertébrés mais bien des araignées, des fourmis, des hyménoptères parasitoïdes et certains autres prédateurs aphidiphages les attaquent (Hodek & Honĕk 1996). Au total, plus de cent espèces animales exploitent les coccinelles (Hodek & Honĕk 1996).

4.3. La cécidomyie prédatrice

Aphidoletes aphidimyza compte parmi les auxiliaires de lutte biologique indigènes à l'Amérique du Nord et à l'Europe (Grasswitz & Burts 1995). C'est un petit diptère dont les larves se nourrissent exclusivement de pucerons (Malais & Ravensberg 1993; Nijveldt 1988) et adoptent un comportement furtif de prédation (Lucas & Brodeur 2001). Les œufs sont pondus séparément ou en petits groupes sous les feuilles au sein des colonies de pucerons (Bouchard & Tourneur 1981; Markkula *et al.* 1985). Juste après l'éclosion, les larves peuvent parcourir une distance linéaire maximale de 63 mm sans s'alimenter (Markkula *et al.* 1985). Leur régime alimentaire spécialisé et leur faible capacité de déplacement les contraignent à vivre à proximité ou à l'intérieur des colonies de pucerons (Markkula *et al.* 1985). Par conséquent, les larves ne changent pas ou rarement de colonies de pucerons au cours de leur développement (Havelka & Zemek 1999) qui dure de 7 à 14 jours selon les conditions du milieu (Jeoung *et al.* 2003).

Parmi les ennemis naturels d'*A. aphidimyza*, on compte des hyménoptères parasitoïdes, des nématodes (Powell & Webster 2004), des coccinelles et des chrysopes (Gardiner & Landis 2007; Voynaud 2008). Ces deux derniers prédateurs sont des prédateurs intraguildes important des œufs et des larves d'*A. aphidimyza* (Lucas *et al.* 1998; Voynaud 2008). Les larves d'*A. aphidimyza* sont très vulnérables, car leurs prédateurs intraguildes sont plus mobiles et de taille supérieure. Une des stratégies de défense des larves d'*A. aphidimyza* consiste à s'éjecter du plant en cas d'attaque (Voynaud 2008). Elles profitent aussi d'un effet de dilution créé par les pucerons. En effet, Lucas et Brodeur (2001) ont démontré que, lorsque la densité de pucerons augmente, la prédation des larves d'*A. aphidimyza* par *Chrysoperla rufilabis* diminue.

Chapitre 3

Contributions de l'auteur et des co-auteurs

Étant le premier auteur de chacun des articles, j'ai conçu et élaboré l'essentiel de ceux-ci. J'ai réalisé, pour chaque article, les modèles mathématiques, les expériences, l'analyse des données, leur interprétation et la rédaction des manuscrits.

Article I. Sentis, A., Hemptinne, J.L., and J. Brodeur. (2012). Using functional response modeling to investigate the effect of temperature on predator feeding rate and energetic efficiency. Oecologia (publié).

Le Dr. Jean-Louis Hemptinne est un spécialiste des relations prédateur-proie. De par son expertise, il a participé activement au développement des idées, à la conception des expériences et à la révision des différentes versions du manuscrit. Le Dr. Jacques Brodeur est à l'origine du projet puisqu'il a obtenu un financement CRSNG Stratégique qui réunissait plusieurs chercheurs au Canada et qui avait pour but d'étudier l'effet des perturbations climatiques sur les plantes, les herbivores et leurs prédateurs à différentes échelles (chambre de croissance et serres). Le Dr. Brodeur a donc assumé les coûts de la recherche. Il a aussi participé à la conception et à l'élaboration du projet, ainsi qu'à la rédaction du manuscrit.

Article II. Sentis, A., Hemptinne, J.L., and J. Brodeur. (2012). How functional response and system productivity modulate intraguild predation.

Le Dr. Jean-Louis Hemptinne a participé au développement de la problématique générale, à la conception des expériences et à la rédaction du manuscrit. Le Dr. Brodeur a assumé le financement et participé à la conception et à l'élaboration du projet. Il a aussi largement contribué à la rédaction du manuscrit.

Article III. Sentis, A., Hemptinne, J.L., and J. Brodeur. (2012). Effects of temperature and prey density on intraguild predation: combining modeling and experimental approaches.

Le Dr. Jean-Louis Hemptinne a participé au développement de la problématique générale, à la conception des expériences et à la rédaction du manuscrit. Le Dr. Brodeur a assumé les coûts de la recherche et participé à la conception et à l'élaboration du projet. Il a aussi largement contribué à la rédaction du manuscrit.

Article IV. Sentis, A., Hemptinne, J.L., and J. Brodeur. (2012). Effects of extreme temperature fluctuations on a plant–herbivore–predator system.

Le Dr. Jean-Louis Hemptinne a participé au développement de la problématique générale, à la conception des expériences et à la rédaction du manuscrit. Le Dr. Brodeur a assumé le financement du projet et participé à la conception et à l'élaboration du projet. Il a aussi largement contribué à la rédaction du manuscrit.

Chapitre 4

Évaluation de l’effet de la température sur le taux de prédation et l'efficacité énergétique d’un prédateur à l’aide d’un modèle de réponse fonctionnelle

Ce chapitre a fait l’objet en 2012 d’une publication dans le journal *Oecologia*,
Sous le titre suivant :

Using functional response modeling to investigate the effect of temperature on predator feeding rate and energetic efficiency

Arnaud Sentis, Jean-Louis Hemptinne et Jacques Brodeur

Résumé

La température, facteur clé pour les organismes poïkilothermes, influence directement leur métabolisme et donc, leur comportement ainsi que leurs traits d’histoire de vie. De nombreuses études ont déterminé les températures optimales et les fenêtres thermiques propres à la survie, au développement et à la reproduction des organismes. Toutefois, peu d'études ont évalué les effets de la température sur les interactions prédateur-proie et calculé les seuils de température qui limitent ces dernières. Dans ce contexte, nous avons développé un modèle de réponse fonctionnelle qui prédit l’effet de la température sur ces interactions et le taux de prédation. Les prédictions du modèle ont ensuite été testées en laboratoire à l’aide d’un système coccinelle-puceron. Tel que le prédit la théorie métabolique de l'écologie, nous avons constaté que le temps de manipulation décroît exponentiellement lorsque la température augmente. Par contre, contrairement à cette théorie, l’efficacité de recherche du prédateur suit une relation en cloche. Un examen du modèle a révélé que les seuils de température pour la prédation dépendent principalement de l’efficacité de recherche du prédateur, ce qui suggère que le taux de prédation est essentiellement déterminé par l’activité de recherche et secondairement par le temps de manipulation des proies. Contrairement aux études antérieures, notre modèle montre que l’intensité de l’interaction prédateur-proie et l'efficacité énergétique (gain d’énergie par rapport aux dépenses énergétiques du métabolisme) du prédateur augmentent avec la température, atteignent un optimum, puis diminuent lorsque les températures continuent de croître. Nous concluons qu’intégrer le concept de fenêtre thermique aux futures études permettrait certainement une meilleure compréhension de la dynamique des populations de prédateurs et de proies. Ceci est essentiel pour augmenter la qualité des prédictions concernant les effets du réchauffement climatique sur les écosystèmes naturels.

Mots clés. Interactions prédateur-proie, modélisation, fenêtre thermique, théorie métabolique de l'écologie, coccinelles, pucerons.

Abstract

Temperature is one of the most important environmental parameters influencing all the biological processes and functions of poikilothermic organisms. Although extensive research has been carried out to evaluate the effects of temperature on animal life histories and to determine the upper and lower temperature thresholds as well as the optimal temperatures for survival, development, and reproduction, few studies have investigated links between thermal window, metabolism, and trophic interactions such as predation. We developed models and conducted laboratory experiments to investigate how temperature influences predator–prey interaction strengths (i.e., functional response) using a ladybeetle larva feeding on aphid prey. As predicted by the metabolic theory of ecology, we found that handling time exponentially decreases with warming, but—in contrast with this theory—search rate follows a hump-shaped relationship with temperature. An examination of the model reveals that temperature thresholds for predation depend mainly on search rate, suggesting that predation rate is primarily determined by searching activities and secondly by prey handling. In contrast with prior studies, our model shows that *per capita* short-term predator–prey interaction strengths and predator energetic efficiency *(per capita* feeding rate relative to metabolism) generally increase with temperature, reach an optimum, and then decrease at higher temperatures. We conclude that integrating the concept of thermal windows in short- and long-term ecological studies would lead to a better understanding of predator–prey population dynamics at thermal limits and allow better predictions of global warming effects on natural ecosystems.

Key words. Predator–prey interactions, models, temperature window, metabolic theory of ecology, ladybeetles, aphids.

Introduction

Temperature is one of the most important environmental parameters influencing all biological process rates and functions. Temperature variations have a determinant and direct effect on ectotherm metabolism and behavior (Bale 2002), and the resulting changes in activities may have cascading effects at population and community levels (Brown *et al.* 2004; Hoekman 2010; Petchey *et al.* 2010). All organisms live within a range of temperatures allowing growth and reproduction; this is called the organism's thermal window (Dixon *et al.* 2009). At the upper and lower thermal limits, the organism's performance decreases due to the limiting capacity for oxygen supply and anaerobic metabolism near the critical temperatures (Pörtner *et al.* 2006; Pörtner & Farrell 2008). Extensive research has been carried out to evaluate the effects of temperature on animal life history and to determine the upper and lower temperature thresholds as well as the optimal temperatures for survival, development, and reproduction (Bale 2002; Dixon *et al.* 2009; Pörtner *et al.* 2006). Although it has long been recognized that different functions have different thermal windows, with active behaviors occurring in narrower windows than passive tolerance, few studies have investigated links between thermal windows and trophic interactions such as predation. This is especially relevant because temperature strongly influences interaction strengths, which have important effects on predator–prey population dynamics (Vasseur & McCann 2005) and community structure (Petchey *et al.* 2010).

The energetic efficiency of an organism determines the amount of energy available for activity, growth, and reproduction, thereby contributing to the organism's overall success. Energetic efficiency is the ratio between energy gain through food assimilation and energy lost through metabolism (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011). According to the metabolic theory of ecology (MTE) (Brown *et al.* 2004), temperature is one of the most important drivers of metabolic activity and, consequently, contributes to determining predator energetic efficiency. Few studies have examined the effects of temperature on predator energetic efficiency. Vucic-Pestic *et al.* (2011) and Rall *et al.* (2010) showed that energetic efficiency decreases with warming while Vasseur and McCann (2005) found the reverse. Although the slope of this relationship remains controversial, there is now evidence that predator energetic efficiency is a major determinant of population stability (Vasseur & McCann 2005). Because predator feeding rate may vary with temperature in a nonlinear way, it is relevant to determine predator energetic efficiency across the thermal window for predation activity as suggested by Englund *et al.* (2011).

A simple model of predator–prey interaction strength is provided by the functional response that describes the relationship between the number of prey available and the number of prey killed by a predator (Holling 1959). Several studies on ectotherms have shown that temperature has a strong effect on functional response; typically, predation increases with warming (Eggleston 1990; Gresens *et al.* 1982; Persson 1986; Thompson 1978; Zamani *et al.* 2006). The functional response mainly depends on two behavioral parameters: search rate (the predator's searching efficiency), and handling time (the time to kill and eat a prey) (Holling 1959). Because biochemical processes of animals largely depend on temperature (Gillooly *et al.* 2001), both search rate and handling time are directly related to ambient temperature. Following MTE, handling time and search rate should exhibit a similar temperature dependence to metabolic rate. It is predicted that search rate would increase and handling time decrease exponentially with warming (Brown *et al.* 2004). This exponential relationship has been well established for handling time (Cave & Gaylor 1989; Flinn 1991; Mack & Smilowitz 1982; Menon *et al.* 2002; Xia *et al.* 2003) but remains unclear for search rate. The relationship between temperature and search rate has been described as being linear, quadratic, or hump-shaped (Cave & Gaylor 1989; Flinn 1991; Mack & Smilowitz 1982; Xia *et al.* 2003). Because an active behavior like searching decreases at extreme temperatures, investigating the effect over a large temperature range is necessary to draw a complete picture. Moreover, it has been recognized that variations in search rate and handling time can induce major changes in population and food-web stability (Brose *et al.* 2006; Rall *et al.* 2008; Williams & Martinez 2004). Recently, Petchey *et al.* (2010) developed a mechanistic model to predict the effect of temperature on food web connectance. They concluded that relative sizes of the activation energies of attack rate and handling time determine whether warming increases or decreases connectance.

Models are useful for studying the effect of temperature on predation because they can predict the functional response for any temperature–prey density combination and may help to understand the underlying mechanisms (e.g., foraging behavior). In this paper, we developed a temperature-mediated functional response model based on predator foraging behavior and following the metabolic theory of ecology. Under laboratory conditions, we investigated the potential effects of low and high temperatures on functional response, search rate, and handling time of ladybeetles feeding on aphids. Using our model, we also determined predator energetic efficiency across a large range of temperatures. The significance for population stability and community structure is briefly discussed.

Materials and methods

Biological system

We studied the functional response of a ladybeetle, *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae), preying on the green peach aphid, *Myzus persicae* Sulzer (Homoptera: Aphididae). *C. maculata*, a common natural enemy of several aphid species in North America (Benton & Crump 1981; Gordon 1985), is a good predator model to study the effect of temperature on functional response since this species has a large distribution and individuals can experience a wide range of temperatures throughout their lifetime in temperate zones (Gordon 1985).

Adult *C. maculata* (more than 4,000) were collected in October 2009 from a field in Saint-Mathieu de Beloeil (45°35'N, 74°45'W, Québec, Canada). Coccinellids were reared in sealed plastic mesh boxes (946 mL; Ziploc®), provided with moistened paper strips, and fed *ad libitum* with pollen, a liver-based artificial diet (Firlej *et al.* 2006), and aphids [*M. persicae*, *Aphis glycines* Matsumura, and *Acyrthosiphon pisum* Harris (Homoptera: Aphididae)]. A colony of *M. persicae*, established from individuals collected in greenhouses from Agriculture and Agri-Food Canada, St-Jean-sur-Richelieu, Québec, Canada, was maintained on sweet pepper plants (*Capsicum annuum* L. cv. Bell Boy). Pepper plants were fertilized twice a week with Nitrophoska (12-4-14) at a concentration of 100 ppm of nitrogen (Plant-Prod, Montréal, QC, Canada). All insects and plants were reared in a growth chamber (Conviron® E15) at 24 ± 1°C, 50–60% relative humidity, 150 µmol $(m^2)^{-1}$ s^{-1} light intensity, and under a 16L:8D photoperiod.

Experiments

We tested the functional response of *C. maculata* at six temperatures [(mean ± SE) 13.9 ± 0.5, 17.6 ± 0.5, 21.7 ± 0.3, 25.8 ± 0.6, 29.4 ± 0.6, 32.8 ± 0.9°C] and under a relative humidity of 70 ± 8% and a photoperiod of 16L:8D. These temperatures cover the range of temperatures allowing the complete development of *C. maculata* (Obrycki & Tauber 1978). During the experiment, temperature and humidity were recorded continuously using Hobo® U12 units. After egg hatching, *C. maculata* larvae were reared at 24°C in Petri dishes (100 × 15 mm) and fed *ad libitum* with green peach aphids until larvae reached the third instar. To standardize the response of tested individuals and stimulate their predatory activity, larvae were starved for 21 h in Petri dishes containing only moistened filter paper. Experimental arenas consisted of a plastic cylinder (20 cm in diameter and 45 cm in height for a surface area of 2,826 cm²) glued to a plastic disc platform. The top of the cylinder and two lateral openings were covered with muslin to allow air circulation. Pepper plants used in experimental arenas were 4 weeks old with four leaves. The apex was removed because it is difficult to see aphids hidden within this plant structure. Third instar aphids (mean weight value ± SE: 0.17 mg ± 0.025) obtained from synchronous cohorts of *M. persicae* were used as prey throughout the experiment. At the onset of the experiment, aphids were transferred to the upper leaves of the plants using a fine camel hair brush. Prey densities were 5, 10, 20, 30, 45, 60, and 90 *M. persicae* per plant. Two hours after the introduction of aphids, a single newly moulted third instar *C. maculata* larva was introduced at the bottom of the stem. After 24 h, the number of remaining aphids was recorded to establish the predation rate. For each aphid density, the experiment was repeated eight times with a predator and four times without (control treatment to assess natural aphid mortality). In addition, 32 third instar *C. maculata* larvae were weighed after 21 h of starvation using a micro-balance (Mettler Toledo MT5). The mean weight value ± SE (4.71 ± 2.28 mg) was used to parameterize the handling time equation.

Statistical analyses and modeling

Data were analyzed using R (v.2.13.1, R Development Core Team, 2011). To examine the functional response of a predator, the first step is to determine the shape of the response curve. To discriminate between type II and type III functional responses, a logistic regression between the proportion of prey eaten (N_e/N_0) and initial prey density (N_0) was performed (Juliano 2001):

$$\frac{N_e}{N_0} = \frac{\exp\,(P_0 + P_1 N_0 + P_2 N_0{}^2 + P_3 N_0{}^3)}{1 + \exp\,(P_0 + P_1 N_0 + P_2 N_0{}^2 + P_3 N_0{}^3)} \qquad \textbf{(1)}$$

where N_e is the number of prey eaten, N_0 is the initial number of prey, and P_0, P_1, P_2, and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively, estimated using the maximum likelihood method (Juliano 2001). If $P_1 > 0$ and $P_2 < 0$, the proportion of prey consumed is positively density dependent, corresponding to a type III functional response. If $P_1 < 0$, the proportion of prey consumed declines monotonically with the initial density of prey, corresponding to a type II functional response (Juliano 2001).

After determining the shape of the response curve, the parameters [handling time (day prey^{-1}) and search rate (0.28 m² day^{-1}; experimental arena volume day^{-1})] were estimated using a nonlinear least-square regression procedure for the Rogers random predator equation (1972):

$$N_e = N_0(1 - e^{-a_1(t - h_1 N_e)}) \tag{2}$$

where $\boldsymbol{N_e}$ is the number of prey eaten, $\boldsymbol{N_0}$ the initial number of prey, $\boldsymbol{t}$ the total experimental time, $\boldsymbol{a}$ the search rate (0.28 m² day^{-1}), and $\boldsymbol{h}$ the handling time (day prey^{-1}). Before fitting the nonlinear least-square regression, we used the package "EMDBOOK" from the R statistical software to solve the Rogers random predator equation (Bolker 2008). This yields:

$$N_e = N_0 - \frac{w(ahN_0 e^{-a(t-hN_0)})}{ah} \tag{3}$$

where w is the Lambert W function (see Bolker 2008 for details).

Based on MTE, handling time depends on body mass, M (mg), and environmental temperature, T (K):

$$h = h_0 M^{b_h} e^{E_h / kT} \tag{4}$$

where $\boldsymbol{h_0}$ is a normalization constant independent of body size and temperature, $\boldsymbol{b_h}$ is an allometric exponent (0.75), $\boldsymbol{E_h}$ is the activation energy (eV) (defined as the average activation energy for the rate-limiting enzyme-catalyzed biochemical reaction of metabolism), and $\boldsymbol{k}$ is Boltzmann's constant (8.62×10^{-5} eV K^{-1}). The value of $\boldsymbol{b_h}$ is assumed to be 0.75 and is derived from the physics of distribution networks in animals (West *et al.* 1997); $\boldsymbol{h_0}$ and $\boldsymbol{E_h}$ are estimated empirically using nonlinear least-square regressions.

Because preliminary results indicated a nonlinear relationship between temperature and search rate, we developed a new model adapted from Briere *et al.* (1999) that accounts for such a nonlinear effect:

$$a(T) = \begin{cases} 0 & \text{if } T \le T_0 \\ b(T - T_0)(T_l - T)^{1/2} & \text{if } T_0 \le T \le T_l \\ 0 & \text{if } T \ge T_l \end{cases} \quad \textbf{(5)}$$

where $\boldsymbol{a}$ is a positive function of temperature, $\boldsymbol{b}$ is an empirical constant, and $\boldsymbol{T_l}$ and $\boldsymbol{T_0}$ are the upper and lower thresholds for search rate, respectively. This model is simple and useful for determining temperature thresholds for searching activity.

To predict the functional response over a wide range of temperatures, we developed a temperature-dependent functional response model in which handling time and search rate were substituted by Eqs. 4 and 5, respectively. These equations were modified from the Rogers random predator equation (1972) (Eq. 2):

$$N_e = N_0(1 - e^{b(T-T_0)(T_l-T)^{1/2}(h_0 M^{b_h} e^{E_h/kT} N_e - t)}) \quad \textbf{(6)}$$

This model was fitted to the entire dataset using a nonlinear least-square regression procedure and the Lambert *W* function (Bolker 2008) to solve the recursive function of *Ne*.

To evaluate the energetic efficiency of *C. maculata*, we used the following equation (Rall *et al.* 2010; Vasseur & McCann 2005; Vucic-Pestic *et al.* 2011):

$$y = \frac{\omega F}{\lambda I} \quad \textbf{(7)}$$

where y is the dimensionless energetic efficiency of the predator, F is the *per capita* energy feeding rate (J h^{-1}), which is equal to the *per capita* biomass feeding rate (mg h^{-1}) multiplied by a weight–energy conversion factor (1 mg wet mass = 7 J; Peters 1986), ω is a temperature-independent assimilation efficiency (0.85 for carnivores; see Rall *et al.* 2010 for details), λ is a constant converting standard metabolic rate into field metabolic rate ($\lambda = 3$; Savage *et al.* 2004), and I is the standard metabolic rate. Based on MTE, we used the null model for metabolic rate (Brown *et al.* 2004):

$$I = i_0 M^{b_i} e^{-E_i / kT} \quad \textbf{(8)}$$

where i_0 is a normalization constant independent of body size and temperature (2.86×10^7 for invertebrates; Brown *et al.* 2004), b_i is an allometric exponent (0.75), E_i is the activation energy for metabolism (0.65 eV; Brown *et al.* 2004), and k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}).

Results

Only 0.5 ± 0.1% (mean ± SE) of the aphids died in the control treatments (without predator), and mortality did not differ among temperatures (Wilcoxon: $\chi^2 = 8.5$, $df = 5$, $P = 0.13$). As a result, we did not correct data for natural aphid mortality in our analyses.

For each temperature, the linear parameters of the logistic regression model were negative and the proportion of aphids eaten decreased when prey density increased, suggesting a type II functional response at each temperature. Typically, predator voracity increased with prey density until reaching a plateau corresponding to the maximum number of prey eaten in 24 h (Fig. 1). This number increased with temperature (Fig. 1).

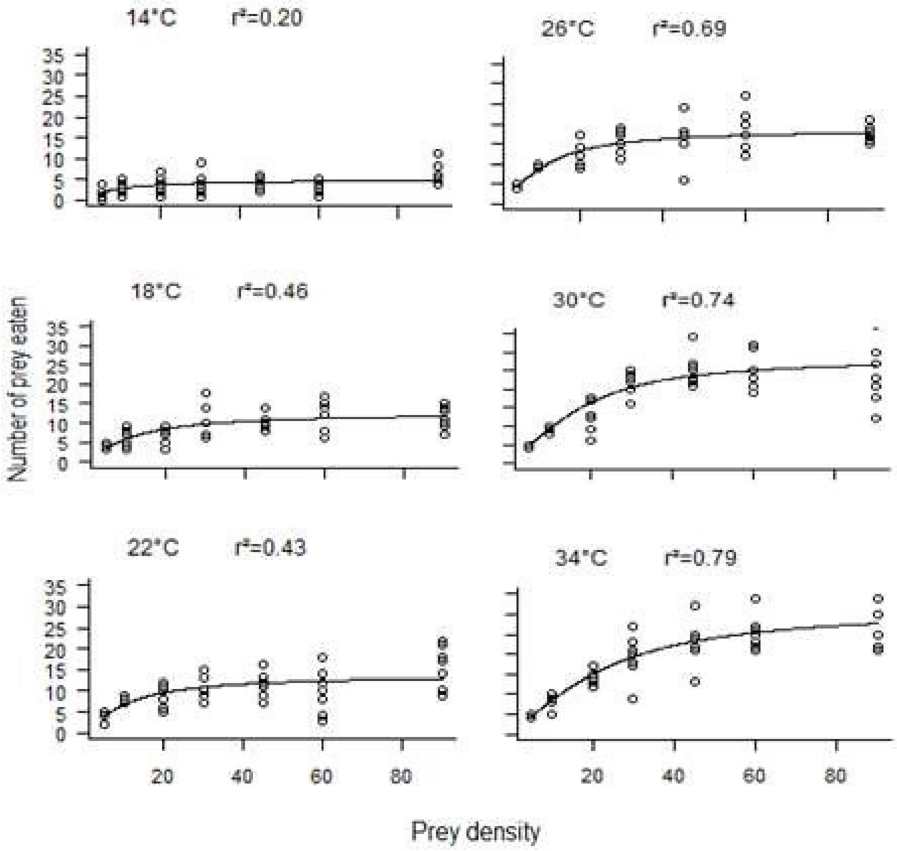

Fig. 1. Functional responses of *Coleomegilla maculata* at seven densities of *Myzus persicae* under six temperatures. The Rogers random predator equation was fitted separately for each temperature. $n = 56$ for all temperature treatments except for 26 and 34°C, where $n = 55$.

Following the identification of the functional response type, the Rogers random predator equation (Eq. 3) was fitted separately for each temperature. The coefficient of determination (r^2) of the Rogers model ranged from 0.2 to 0.79, with a larger variability in predation rate at the lower temperatures (14, 18, and 22°C) than at the higher temperatures (26, 30, and 34°C), as shown in Fig. 1.

Plots of both estimated values of handling time and search rate versus temperature indicate that Eqs. 4 and 5, respectively, are appropriate for describing these two parameters (Fig. 2). As predicted by MTE, handling time decreases exponentially with warming (Fig. 2a, Table 1). In contrast, search rate increases with warming, reaches an optimum, and then decreases at higher temperatures (Fig. 2b, Table 1).

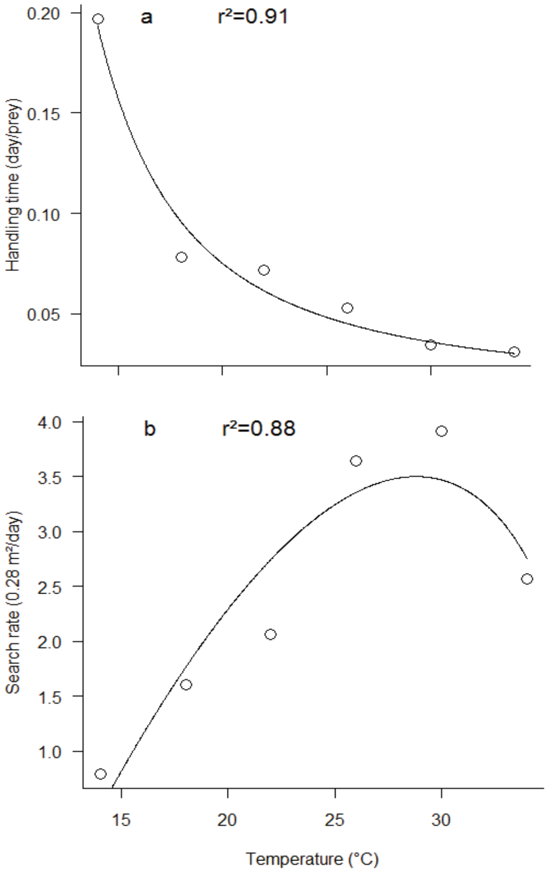

Fig. 2. Relationships between **(a)** temperature and handling time and **(b)** temperature and search rate of *C. maculata*. For handling time, $h = 8.93 \times 10^{-18} M^{0.75} e^{0.9/kT}$, where M is the predator body mass (4.71 mg), T (K) is the environmental temperature, and k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}) ($r^2 = 0.91$, $P < 0.0001$, $n = 6$). For search rate, $a = 0.077\ (T-285.71)\ (309.86-T)^{1/2}$ ($r^2 = 0.88$, $P < 0.0001$, $n = 6$).

Table 1. Estimates of *C. maculata* search rate and handling time (mean ± SE and *P* value) using the Rogers random predator equation at six temperatures.

Temperature (°C)	**Search rate (0.28 m² day^{-1})**		**Handling time (day prey^{-1})**	
	Mean ± SE	*P* value	Mean ± SE	*P* value
13.9	0.788 ± 0.367	0.0365	0.197 ± 0.023	< 0.0001
17.6	1.603 ± 0.496	0.0021	0.078 ± 0.006	< 0.0001
21.7	2.064 ± 0.756	0.0085	0.072 ± 0.006	< 0.0001
25.8	3.638 ± 1.146	0.0025	0.053 ± 0.003	< 0.0001
29.4	3.916 ± 1.293	0.0038	0.034 ± 0.003	< 0.0001
32.8	2.569 ± 0.592	< 0.0001	0.031 ± 0.002	< 0.0001

To predict the functional response of *C. maculata* feeding on *M. persicae* over a range of temperatures and to obtain better estimations of model parameter values, we fitted a temperature-mediated functional response equation (Eq. 6) to the entire dataset using nonlinear least-squares regression ($r^2 = 0.80$, $df = 329$, $P < 0.0001$, $n = 334$). Estimates and standard errors for T_0, T_l, b, E_h, and h_0 are 285.2 ± 0.24 (K), 311.25 ± 0.31 (K), 0.11 ± 0.023, 0.61 ± 0.038 (eV), and $9.57 \times 10^{-13} \pm 1.41 \times 10^{-13}$, respectively.

Based on model predictions, the number of prey eaten increases with increasing prey density (Fig. 3). Maximum predation increases with warming but decreases rapidly at extreme temperatures (Fig. 3). The model indicates that the lower and upper temperature thresholds for predation rate are 12.05 ± 0.24 and 38.1 ± 0.31°C, respectively.

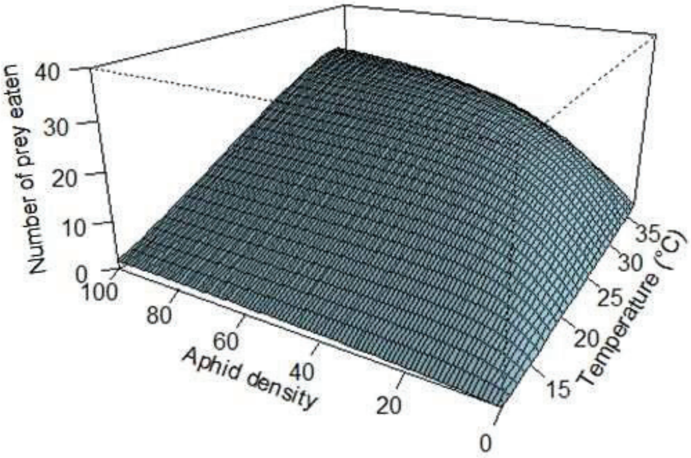

Fig. 3. Three-dimensional contour plot showing the effect of *M. persicae* density and temperature on the number of *M. persicae* eaten by *C. maculata* larvae.

According to the predation rate model (Fig. 3), predator energetic efficiency increases with warming, reaches an optimum, and then decreases rapidly at higher temperatures (Fig. 4). Energetic efficiency always increases with prey density, which is consistent with the classical functional response equation (Holling 1959; Rogers 1972).

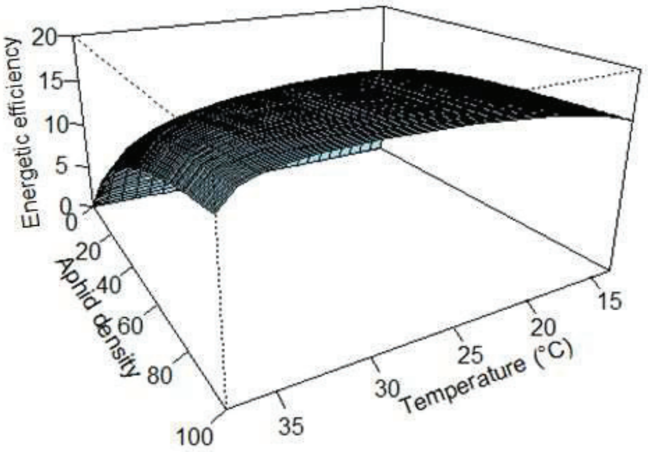

Fig. 4. Three-dimensional contour plot showing the effect of *M. persicae* density and temperature on the energetic efficiency *C. maculata* larvae.

Discussion

Temperature clearly influenced the magnitude of the response of *C. maculata* to *M. persicae* density (Fig. 1). As previously reported for insects, crabs, and fishes (Eggleston 1990; Gresens *et al.* 1982; Persson 1986; Thompson 1978; Zamani *et al.* 2006), the proportion of prey eaten generally increased with warming. As suggested by Rall *et al.* (2010) and Vucic-Pestic *et al.* (2011), this pattern would strengthen short-term predator–prey interactions when prey growth rate and prey density are low. Of particular interest in our study, we (1) showed that the relationship between temperature and interaction strength or predator energetic efficiency is non-linear when considering a large gradient of temperatures, (2) provided a mechanistic link between temperature and some components of predation behavior (e.g., handling time, search rate), and (3) developed a model to predict temperature thresholds for predation activity that can be used to forecast short-term interaction strength and predator energetic efficiency across a large range of temperatures. Our study contributes towards an improved general understanding of temperature effects on predator–prey interactions by introducing the concept of thermal window into a basic model. Such a model describes the behavior of predators in a more realistic environment, i.e. across a large gradient of temperatures.

As predicted by MTE and reported in previous studies (Jalali *et al.* 2010b; Zamani *et al.* 2006), we observed an exponential decrease of handling time with warming (Fig. 2). Moreover, the estimated energy activation for handling time (0.61 ± 0.04 eV) was not different to the one predicted by metabolic theory (0.65 eV). For many predators, prey handling is driven by digestion (Jeschke *et al.* 2002), which depends on metabolism. This is especially true for the 24 h period of our experiment, where handling processes such as killing and ingesting prey are negligible when compared to digestion (Jeschke *et al.* 2002). Our results are consistent with MTE, but the difference between handling and digestion time remains to be explored.

Contrary to MTE, we found that *C. maculata* search rate follows a hump-shaped relationship with temperature (Fig. 2), indicating that foraging activity was reduced at extreme temperatures; this has been reported in prior studies (Cave & Gaylor 1989; Englund *et al.* 2011; Flinn 1991; Mack & Smilowitz 1982; Messenger 1968). This may result from temperature-related changes in predator metabolism: the temperature must be high enough to reach the threshold for metabolic activity, whereas temperatures that are too high reduce metabolic reaction rates through catabolism (Davis *et al.* 2006; Gillooly *et al.* 2001). Thus, the effects of increasing temperature on search rate should be different from a simple exponential relationship when a wide range of temperatures is considered. As was found in studies conducted over a small temperature range (Thompson 1978; Xia *et al.* 2003; Zamani *et al.* 2006), we found that the first section of this hump-shaped curve (lower temperatures) is well described by an exponential or linear function of temperature. However, our results suggest that search rate should be measured over a wider temperature range to include decreasing search rates at high temperatures. This decrease has an important effect on predation rate and, consequently, on the strength of trophic interactions and population stability (Persson *et al.* 1998; Vasseur & McCann 2005).

We developed a new model expressing handling time and search rate as functions of temperature. This model is parsimonious, provides a good estimate of *C. maculata* functional response (r^2 = 0.80), and can predict functional responses for any temperature–prey density combination. The model predicts that short-term interaction strengths (i.e., predation rate) increase with warming, reach an optimum, and then decrease at higher temperatures (Fig. 3). In contrast to other studies reporting an increase in predation rate with warming (Eggleston 1990; Vucic-Pestic *et al.* 2011; Zamani *et al.* 2006), we found that the effect of temperature can be nonlinear (Fig. 3). Because the decrease in predation rate occurs for temperatures close to the thermal limits (Fig. 3), a large range of temperatures should be analyzed to improve predictions for predator–prey dynamics. Our results suggest that classical functional response models such as the Holling disc (1959) or Rogers random search (1972) equations should be improved by a temperature-mediated functional response equation to produce more realistic population growth models.

Our model prediction reveals that the predator functional response is limited in a range of temperatures. Our model requires few parameters and can predict temperature thresholds for predation activity. The lower temperature threshold predicted for *C. maculata* predation activity is 12.05°C, which is consistent with field observations (Elliott *et al.* 2000; Honěk 1985) and laboratory observations (Giroux *et al.* 1995) on *C. maculata* and other aphidophagous Coccinellidae. For the upper temperature threshold, we found that predation rate is nil at 38.1°C. Very few studies have examined this threshold in coccinellids, although Soares *et al.* (2003) reported that the maximum temperature for predation activity for two phenotypes of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) were 36.2 and 31.9°C in Petri dishes. Our model provides a reliable estimation of temperature thresholds in coccinellids and can be used to determine such thresholds for other predator–prey interactions in arthropods. An analysis of the model reveals that the upper and lower temperature thresholds depend mainly on the search rate equation. This suggests that predation rate is primarily determined by searching activities and secondly by prey handling. This should be especially true for aphidophagous predators: since aphids are patchily distributed, the first predation step is to find an aphid colony.

Dixon *et al.* (2005) estimated that the mean lower developmental threshold (LDT) for 22 species of Coccinellidae (including *C. maculata*) is 9.95 ± 0.0043°C. For *C. maculata*, the estimated LDT is 11.3 ± 0.6°C (Obrycki & Tauber 1978). Unfortunately, upper developmental thresholds for *C. maculata* have never been estimated. Published upper developmental thresholds for aphidophagous coccinellids vary from 30 to 35°C for *A. bipunctata* and *Propylea dissecta* Mulsant, respectively (Jalali *et al.* 2010a; Omkar 2004). In the present study, predation occurs between 12.05 and 38.1°C. Comparing temperature ranges for predation and for development reveals that upper and lower temperature thresholds for *C. maculata* predation are higher than those for development. The same comparison could be done for *H. axyridis* (LDT is 10.5°C, Schanderl *et al.* 1985 and the lower temperature threshold for activity is 12°C, Ongagna *et al.* 1993) and for *C. septempunctata* (LDT is 10.9–13.9°C, Obrycki *et al.* 1997; Xia *et al.* 1999 and the lower temperature threshold for locomotion is 13–15°C, Honěk 1985). This highlights the need to include dependent functional responses in dynamic population models because differences in temperature thresholds for different traits can modify predictions of dynamic population models.

As is the case for any laboratory study, our small-scale, short-term experiments have a number of drawbacks. They were conducted in an artificial environment that has little in common with the natural foraging conditions usually experienced by coccinellids in nature. For one thing, we standardized coccinellid and aphid size, but predator–prey size ratio has an important effect on predator foraging capacity (Persson *et al.* 1998; Vucic-Pestic *et al.* 2010). Other factors such as multiple prey and/or predator species interactions and experimental conditions (e.g., arena size, plant architecture, humidity) typically modify predation rates (Carter *et al.* 1984; Giroux *et al.* 1995; Xia *et al.* 2003). We did not consider long-term temperature effects such as thermal adaptations that should also modify the effect of temperature on metabolism and predation rate. However, we think that our approach presents a reliable and simple mechanistic null model of temperature effects on predator–prey interactions to which additional factors may be added.

Our results suggest that predator energetic efficiency (i.e., prey ingestion relative to metabolism) depends on prey density and temperature. It increases together with prey density and reaches a maximum as predicted by the functional response equation (Fig. 4). This is to be expected since ingestion rate is directly related to predation rate, which increases with prey density. Previous studies reported that energetic efficiency can only increase (Vasseur & McCann 2005) or decrease (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011) with warming. In contrast, we observed both an increase and a decrease in energetic efficiency of *C. maculata* within the temperature range we investigated (Fig. 4). At lower temperatures, the energetic efficiency increases due to a lower metabolic demand relative to the higher ingestion rate. At higher temperatures, the predator energetic efficiency decreases due to a stronger increase in the metabolic demand and a decrease in ingestion rate. Our results reveal the existence of thermal limits and optima for prey ingestion that allow for both an increase and a decrease in energetic efficiency. According to the Vasseur and McCann model (2005), our results further suggest that population stability would decrease at lower temperatures and increase at higher temperatures. Taken together, this evidence suggests that predator–prey systems are very sensitive to temperature and that different responses can be observed depending on the intensity of warming. As suggested by other studies (Jones *et al.* 1998; Petchey *et al.* 1999; Voigt *et al.* 2003), higher trophic levels are more sensitive to climatic conditions, and high temperatures may induce starvation because predators would be unable to ingest sufficient food to outweigh metabolic loss (Rall *et al.* 2010; Vucic-Pestic *et al.* 2010). Such scenarios depend on predator sensitivity to temperature (Petchey *et al.* 1999), and our results suggest that they would vary as a function of the thermal optima for energetic efficiency.

Our study provides a simple behavioral model to predict temperature thresholds and predator functional response over a wide range of temperatures for predation activity. In contrast to MTE theory, we found that the search rate follows a hump-shaped relationship with temperature and sets the limit of predation activity. Our results further suggest that the concept of thermal windows should be applied to predator–prey interactions and population dynamics because temperature effects close to thermal limits can be different than for middle-range temperatures. Integrating the concept of thermal windows could lead to a better understanding of interaction strengths at thermal limits and of global warming effects on natural ecosystems.

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Chapitre 5

Comment la réponse fonctionnelle et la productivité du système influencent-elles la prédation intraguilde ?

Cet article sera soumis à la revue *Ecology*,
Sous le titre suivant :

How functional response and system productivity modulate intraguild predation

Arnaud Sentis, Jean-Louis Hemptinne et Jacques Brodeur

Résumé

Plusieurs modèles ont été développés pour prédire l'effet de la productivité d'un système sur l'intensité de la prédation intraguilde et sur la coexistence des protagonistes. Une composante importante de ces modèles est la réponse fonctionnelle des prédateurs puisque des variations dans sa forme ou dans la valeur de ses paramètres influencent fortement les interactions trophiques et, par conséquent, la stabilité et la persistance des communautés. Les modèles précédemment publiés ont principalement utilisé les réponses fonctionnelles de type I et II développées par Holling mais, à notre connaissance, aucune étude empirique n'a jamais examiné lequel de ces deux modèles décrit le mieux la réponse fonctionnelle d'un prédateur intraguilde. Cette question est importante car le type de réponse fonctionnelle détermine le gain énergétique du prédateur et, par conséquent, sa réponse numérique et sa reproduction, ce qui se répercute sur la dynamique des populations et des réseaux trophiques. Nous avons donc développé un modèle linéaire (type I) et un modèle non-linéaire (type II) de réponse fonctionnelle pour prédateur intraguilde. Nous les avons ensuite paramétrés à l'aide d'observations réalisées sur un système plante-puceron-prédateur afin de générer des prédictions spécifiques à ce système. Par la suite, nous avons testé ces prédictions en manipulant la densité de pucerons dans des enceintes expérimentales. Nous avons constaté que (1) le nombre total de proies consommées par le prédateur intraguilde (coccinelle) augmente avec la densité de proies extraguildes (pucerons) pour atteindre un plateau et (2) une augmentation de la densité de proies extraguildes offre une protection à la proie intraguilde par un effet de dilution, ce qui diminue l'intensité de la prédation intraguilde. Les prédictions du modèle non-linéaire correspondaient bien aux observations expérimentales tandis que le modèle linéaire surestimait généralement le nombre total de proies consommées par le prédateur intraguilde et l'intensité de la prédation intraguilde, car ce dernier ignore d'importantes caractéristiques comportementales du prédateur intraguilde telles que le temps de manipulation. Nous concluons que le modèle non-linéaire prédit adéquatement l'intensité de la prédation intraguilde et permet de mieux comprendre comment la productivité du système et les variations du temps de manipulation et de l'efficacité de recherche du prédateur influencent les interactions intraguildes.

Mots clés. Interactions prédateur-prédateur, modélisation, densité de proies, effet de dilution, puceron, coccinelle, cécidomyie prédatrice.

Abstract

Several models have been developed to predict the effect of system productivity on the occurrence of intraguild predation and the coexistence of interacting species of prey and predators. An important component of these models is the predator functional response because variations in its shape or parameter values can modify the outcomes of interactions and thereby food web stability and persistence. Models have mainly used Holling type I and type II functional responses, but to our knowledge no empirical study has examined which one best describes the functional response of an intraguild predator. This question is important because the type of functional response determines the predator's energy intake and thus its reproduction and numerical response, which influence population fluctuations and food web dynamics. In this study, we first developed two functional response models for intraguild predators, one linear and one nonlinear. We next used a plant–aphid–predator mesocosm to parameterize the models and generate specific predictions about predator–prey interactions. We then tested our models by manipulating aphid density within an experimental arena. We found that (1) the total number of prey eaten by the intraguild predator (coccinellid) increases with extraguild prey density (aphid) to reach a maximum, (2) an increase of extraguild prey density is associated with a decrease in the intensity of intraguild predation through a dilution effect that provides protection to the intraguild prey (predatory midge). The predictions of the nonlinear functional response model fit very well with experimental observations whereas the linear model generally overestimates the total number of prey eaten by the intraguild predator and the intensity of intraguild predation, mainly because important behavioral characteristics such as handling time are ignored. The nonlinear model is thus a good predictor of intraguild predation and allows an understanding of how system productivity and variations in search rate or handling time influence the occurrence of intraguild predation.

Key words. Predator–prey interactions, prey density, dilution effect, aphid, ladybeetle, predatory midge.

Introduction

Intraguild predation (IGP) occurs when two predator species compete for a common resource and also feed on each other (Polis *et al.* 1989). IGP is a widespread interaction in natural and managed ecosystems (Arim & Marquet 2004) that may influence the structure and stability of communities (Holt & Polis 1997; Morin 1999; Mylius *et al.* 2001; Vance-Chalcraft *et al.* 2007) and, from an applied perspective, the outcome of biological control and the management of endangered or exotic invasive species (Müller & Brodeur 2002; Rosenheim *et al.* 1995; Rosenheim 1998; Straub *et al.* 2008; Vance-Chalcraft *et al.* 2007). Following the publication of a general theory of IGP by Holt and Polis (1997), several models and empirical studies have investigated the nature and prevalence of IGP in diverse terrestrial and aquatic communities. An important component of this theory is the effect of ecosystem productivity on the coexistence of competing organisms (Borer *et al.* 2003; Diehl & Feissel 2000; 2001; Holt & Polis 1997; Morin 1999; Mylius *et al.* 2001). According to the theory, only the intermediate predator (i.e., the intraguild prey; IG prey) should persist at low productivity because it has a better capacity to exploit resources than the top predator (i.e., the intraguild predator; IG predator), whereas the latter should drive the IG prey to extinction at high productivity through a combined effect of competition and predation. Therefore, IGP theory predicts that coexistence can only occur at intermediate productivity levels (Borer *et al.* 2003; Borer *et al.* 2007; Diehl & Feissel 2000; Holt & Polis 1997; Mylius *et al.* 2001), but few empirical studies have validated this prediction (Diehl & Feissel 2000; 2001). In contrast to the theory, many field and laboratory experiments have reported cases of coexistence over a large gradient of productivity (Amarasekare 2000; Amarasekare 2007; 2008; Borer *et al.* 2003; Brodeur *et al.* 2002; Lawler & Morin 1993; Lucas & Rosenheim 2011; Morin 1999). Moreover, IGP generally tends to decrease as the density of the shared or extraguild (EG) prey increases (Lucas & Rosenheim 2011), suggesting that at high productivity (typically characterized by high EG prey density) IGP may not be common and coexistence possible.

The mismatch between model predictions and empirical observations suggests that models do not correctly translate some important features of trophic and guild interactions occurring in food webs. We hypothesized that this drawback partially originates from model assumptions about the functional response of the intraguild predator. The functional response denotes the relationship between prey density and predation rate (Holling 1959). Earlier studies have pointed out that the type of functional response or small variations in its parameter values can have important consequences on populations dynamics and food webs (Briggs & Borer 2005; McCann & Hastings 1997; Rall *et al.* 2008; Uchida *et al.* 2007; Williams 2008). IGP models assuming a linear functional response for the IG predator lead to predictions of high extinction probability of the IG prey under conditions of high productivity (Borer *et al.* 2003; Borer *et al.* 2007; Briggs & Borer 2005; Diehl & Feissel 2000; Hall 2011; Holt & Polis 1997). In the linear functional response, the number of prey eaten by predators at high prey density is largely overestimated as is the energy intake; this allows too much energy for reproduction and thus a numerical response that leads to strong population fluctuations and instability (McCann & Hastings 1997; McCann *et al.* 1998). In contrast, the predation rate in nonlinear functional response models reaches a maximum at high prey densities that limits energy intake and thus reproduction and the numerical response. Accordingly, this would result in a weaker interaction that should decrease IGP intensity and thereby the probability of IG prey extinction (Abrams & Fung 2010; McCann & Hastings 1997; McCann *et al.* 1998). Therefore, evaluating differences between the linear and nonlinear functional response models is crucial for deepening our understanding of IGP interactions across a productivity gradient.

In this study, our objective was to compare predictions of the linear and nonlinear functional response models examining IG interactions across a gradient of extraguild prey density. We first developed both models for general IG interactions and next used a plant–aphid–predator mesocosm system to parameterize models and generate specific predictions. Finally, we tested model predictions by manipulating aphid density within our experimental system.

Models

The nonlinear model

Most functional response models are based on the Holling type II equation (1959), also known as the disc equation, because it adequately describes the behavior of the vast majority of predators (Jeschke *et al.* 2002). However, this model becomes invalid when a predator removes a substantial proportion of prey that are not replaced, which is a common feature of functional response experiments (Juliano 2001). In such a case, a modification of the disc equation proposed by Rogers (Rogers 1972), and known as the random predator equation, should be used:

$$N_e = N_0 \times (1 - e^{-a(t - hN_e)}) \qquad \textbf{(1)}$$

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

Adding an IG prey to a simple prey–predator food chain can affect the number of extraguild prey eaten by the IG predator in a number of ways. For instance, the pursuit, capture, and consumption of IG prey reduce the amount of time available for encountering EG prey and vice versa. This effect can be included in the basic type II functional response (Eq. 1) as follows (Colton 1987):

$$N_{eg} = N_{0eg} \times (1 - e^{-a_{eg}(t - h_{eg}N_{eg} - h_{ig}N_{ig})}) \qquad \textbf{(2)}$$

$$N_{ig} = N_{0ig} \times (1 - e^{-a_{ig}(t - h_{ig}N_{ig} - h_{eg}N_{eg})}) \qquad \textbf{(3)}$$

where the subscripts refer to the two prey types: *eg* (extraguild) and *ig* (intraguild). N_{eg} and N_{ig} are the number of EG and IG prey eaten by the IG predator, respectively.

The total number of prey eaten by the IG predator is:

$$N_{eg} + N_{ig} = N_{0eg} \times (1 - e^{-a_{eg}(t - h_{eg}N_{eg} - h_{ig}N_{ig})}) + N_{0ig} \times (1 - e^{-a_{ig}(t - h_{ig}N_{ig} - h_{eg}N_{eg})}) \textbf{(4)}$$

In this model, the IG predator can feed on both the EG prey (with attack rate a_{eg}) and the IG prey (with attack rate a_{ig}). The difference between the search rates determines the preference of the IG predator for one of the prey types (if $a_{eg} > a_{ig}$, then the IG predator prefers the EG prey and vice versa). Note that search rates are independent of prey density, which means that predators do not switch from one prey to the other.

The linear model

The only difference with the nonlinear model is that, in linear functional response models, the predator spends all its time searching for prey (i.e., handling time is assumed to be null). Setting the handling time value as null in Eqs. 2 and 3 yields:

$$N_{eg} = N_{0eg} \times (1 - e^{-a_{eg}t}) \tag{5}$$

$$N_{ig} = N_{0ig} \times (1 - e^{-a_{ig}t}) \tag{6}$$

Then, the total number of prey eaten by the IG predator is:

$$N_{eg} + N_{ig} = N_{0eg} \times (1 - e^{-a_{eg}t}) + N_{0ig} \times (1 - e^{-a_{ig}t}) \tag{7}$$

Following Eq. 7, the total number of prey eaten by the IG predator ($N_{eg} + N_{ig}$) increase linearly with prey densities (N_{0eg} and N_{0ig}).

In the next section, we adapt these two general models to our biological system. Because the general and specific model predictions are similar, we only detailed one of them in the next section.

Application of the two models to aphid predators

Ubiquitous and abundant in a majority of terrestrial ecosystems, aphids are among the most important pests of temperate agricultural zones (Blackman & Eastop 2000). Their colonies rapidly grow and decrease, and are exploited by a large number of predator, parasitoid and pathogen species (Brodeur & Rosenheim 2000; Dixon 1977). Because aphid populations are patchily distributed in the habitat, and because most species of predators and parasitoids numerically respond to aphid density and tend to aggregate in densely populated patches (Chacón & Heimpel 2010; Turchin & Kareiva 1989), aphids and the guild of their consumers constitute excellent models to explore food web interactions, including IGP, a very common interaction among aphidophagous predators and parasitoids (Brodeur & Rosenheim 2000; Gagnon *et al.* 2011; Lucas 2005). In the present study, under laboratory conditions, we studied interactions between the green peach aphid *Myzus persicae* Sulzer (Homoptera: Aphididae) (extraguild prey), the spotted ladybeetle *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae) (intraguild predator), and the predatory midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) (intraguild prey). The ladybeetle is a generalist predator that actively searches for prey while the larva of the predatory midge specializes on aphids and displays a furtive hunting behavior that does not trigger prey defensive response (Lucas & Brodeur 2001). IGP is asymmetric as *A. aphidimyza* cannot feed on *C. maculata*. These three insect species have overlapping niches and may coexist in nature (Boiteau 1983).

Aphidoletes aphidimyza larvae live within the aphid colony and move slowly. We therefore assumed a similar search rate for *C. maculata* exploiting either intra- or extraguild prey (i.e. $a_{eg} = a_{ig}$).

The nonlinear model

Setting $a_{eg} = a_{ig}$ in Eq. 4 yields to:

$$N_{eg} + N_{ig} = (N_{0eg} + N_{0ig}) \times (1 - e^{-a_{eg}(t - h_{eg}N_{eg} - h_{ig}N_{ig})}) \qquad \textbf{(8)}$$

Using the Lambert *W* function (Corless *et al.* 1996) to solve this recursive function of N_{eg} and N_{ig} yields to (see Annex 1 for calculation details):

$$N_{eg} + N_{ig} = (N_{0eg} + N_{0ig}) \times (1 - \frac{w(a_{eg}(h_{eg}N_{0eg} + h_{ig}N_{0ig}) \times e^{-a_{eg}(t - h_{eg}N_{0eg} - h_{ig}N_{0ig})})}{a_{eg}(h_{ig}N_{0ig} + h_{eg}N_{0eg})}) \qquad \textbf{(9)}$$

For the number of IG prey eaten, assuming a similar search rate for *C. maculata* when exploiting IG or EG prey in Eq. 3, yields:

$$N_{ig} = N_{0ig} \times (1 - e^{-a_{eg}(t - h_{ig}N_{ig} - h_{eg}N_{eg})}) \qquad \textbf{(10)}$$

Using the Lambert *W* function (Corless *et al.* 1996) to solve this recursive function of N_{eg} and N_{ig} yields:

$$N_{ig} = N_{0ig} \times (1 - \frac{w(a_{eg}(h_{eg}N_{0eg} + h_{ig}N_{0ig}) \times e^{-a_{eg}(t - h_{eg}N_{0eg} - h_{ig}N_{0ig})})}{a_{eg}(h_{ig}N_{0ig} + h_{eg}N_{0eg})}) \qquad \textbf{(11)}$$

The linear model

For the total number of IG prey eaten, assuming a similar search rate for *C. maculata* when exploiting IG or EG prey in Eq. 7, yields:

$$N_{eg} + N_{ig} = (N_{0eg} + N_{0ig}) \times (1 - e^{-a_{eg}t}) \qquad \textbf{(12)}$$

Similarly, for the number of IG prey eaten, setting $a_{eg} = a_{ig}$ in Eq. 6 yields:

$$N_{ig} = N_{0ig} \times (1 - e^{-a_{eg}t}) \qquad \textbf{(13)}$$

Comparison of the predictions of both models

Because search rate and handling time are assumed constant and null, respectively, the linear model (Eq. 12) predicts that the total number of prey eaten by *C. maculata* increases linearly with *M. persicae* and *A. aphidimyza* densities (Fig. 1a). In contrast, the nonlinear model (Eq. 8) predicts that the total number of prey eaten by *C. maculata* increases with both *M. persicae* and *A. aphidimyza* densities but reaches an asymptote at higher prey densities because the predator is limited by the time available for handling prey (Fig. 1b).

Following the linear model prediction (Eq. 13), the number of IG prey eaten only depends on IG predator search rate and IG prey density (Fig. 2a). In contrast, the nonlinear model predicts that the number of IG prey eaten decreases as the density of extraguild prey increases (Fig. 2b and Eq. 10). Note that Eqs. 13 and 10 are similar as N_{eg} and N_{ig} approach the origin:

$$\lim_{\substack{N_{eg}\to 0\\ N_{ig}\to 0}}\left(1-e^{-a_{eg}(t-h_{eg}N_{eg}-h_{ig}N_{ig})}\right)=1-e^{-a_{eg}t} \tag{14}$$

In other words, the predictions of both models are similar at lower prey densities but predictions diverge more and more as prey densities increase.

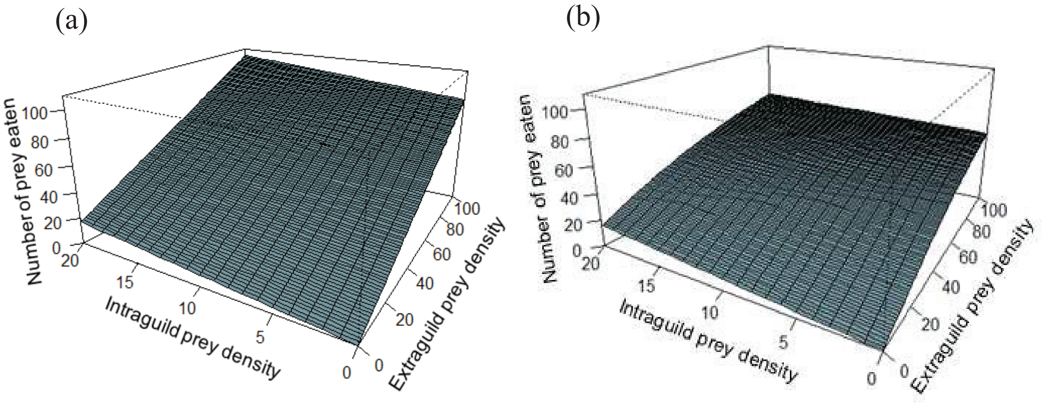

Fig. 1. Total number of prey eaten by an intraguild predator as a function of intra- and extraguild prey densities. **(a)** Predictions of the linear functional response model derived from Eq. 7. **(b)** Predictions of the nonlinear functional response model derived from Eq. 4. Parameter values are $t = 1$, $a_{eg} = a_{ig} = 2$, and $h_{eg} = h_{ig} = 0.01$.

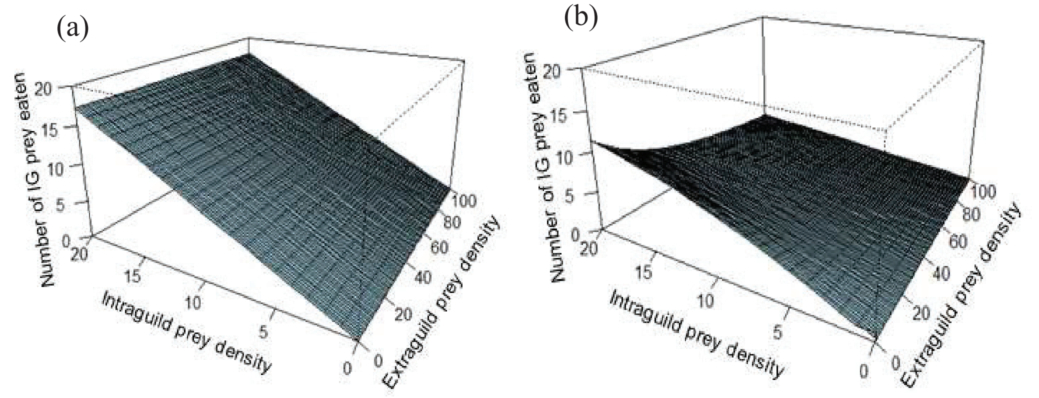

Fig. 2. Number of intraguild prey eaten by intraguild predator as a function of intra- and extraguild prey densities. **(a)** Predictions of the linear functional response model derived from Eq. 13. **(b)** Predictions of the nonlinear functional response models derived from Eq. 11. Parameter values are $t = 1$, $a_{eg} = 2$, and $h_{eg} = h_{ig} = 0.01$.

Only three parameters are needed to generate model predictions: search rate for *M. persicae* (a_{eg}) and handling time for both *M. persicae* (h_{eg}) and *A. aphidimyza* (h_{ig}). Sentis *et al.* (Chapter 4) estimated mean values (± SE) of a_{eg} as 2.064 ± 0.756 (0.28 m² day^{-1}) and h_{eg} as 0.072 ± 0.006 (day prey^{-1}) at 22°C. Note that 0.28 m² corresponds to the area of the experimental arena, so 0.28 m² day^{-1} is equivalent to arena day^{-1}. The following two experiments were designed to estimate the third parameter, h_{ig} (Experiment 1) and test the predictions (Eqs. 9, 11, 12, and 13) of both models (Experiment 2).

Materials and methods

About 4,000 adult *C. maculata* were collected in October 2009 in a field at Saint-Mathieu-de-Beloeil (45°35'N, 74°45'W, Québec, Canada), brought back to the laboratory, and reared in sealed plastic mesh boxes (946 mL; Ziploc®) containing moistened paper strips as a source of water. Coccinellids were fed *ad libitum* with pollen, a liver-based artificial diet (Firlej *et al.* 2006), and aphids (*M. persicae*, *Aphis glycines* Matsumura, and *Acyrthosiphon pisum* Harris). For these experiments, a colony of *M. persicae*, established from individuals collected in greenhouses of Agriculture and

Agri-Food Canada, St-Jean-sur-Richelieu Québec, Canada, was maintained on sweet pepper plants (*Capsicum annuum* L. cv. Bell Boy). Pepper plants were fertilized twice a week with a solution of Nitrophoska ® (12-4-14) with a nitrogen concentration of 100 ppm (Plant-Prod, Montréal, Canada). All insects and plants were reared in a growth chamber (Conviron® E15) at 24 ± 1°C, 50–60% relative humidity, 150 µmol m^{-2} s^{-1} light intensity, and under a 16L:8D photoperiod. During the experiments, temperature and humidity were recorded continuously using Hobo U12 units (Hobo®).

Experiment 1. Handling time for *A. aphidimyza* (h_{ig})

The first experiment was designed to measure *C. maculata* handling time for *A. aphidimyza* (h_{ig}) by direct observation. The experiment was conducted at 22 ± 1°C and under a relative humidity of 70 ± 8%. After hatching, *C. maculata* larvae were reared at 24°C in Petri dishes (100 × 15 mm) and fed green peach aphids *ad libitum* until they reached the 3rd instar. The larvae were held in Petri dishes lined with moistened paper filter and starved for 21 h prior to the experiment to standardize their hunger drive. To standardize prey size, *A. aphidimyza* females were allowed to oviposit for 10 h on a pepper plant infested by *M. persicae*. At the end of this period, females were removed and plants kept aside until eggs hatched and larvae reached 1.3 mm in length (on average 72 h after hatching). Predatory midge larvae were then isolated in a Petri dish (40 × 12 mm) lined with a thin layer of agar (1.5% concentration) covered with a disk of pepper leaf (40 × 12 mm). They were allowed to acclimatize to these conditions for 30 minutes. A single *C. maculata* larva was next introduced into the Petri dish, and its activity was recorded using an HD camera (Sony HDR-XR500©). If the ladybeetle did not attack a midge larva after 4 h, recording was interrupted. We viewed videotapes to measure handling time, defined as the time interval from the beginning of an attack of *C. maculata* on *A. aphidimyza* to the moment when the ladybeetle finished eating. In all replicates, no attack failed and *C. maculata* never moved away before entirely consuming its prey. There were twelve replicates.

Experiment 2. Testing model predictions

The second experiment was designed to test predictions of the two functional response models (Eqs. 9, 11, 12, and 13) by recording the total number of prey eaten by a *C. maculata* larva and the frequency of IGP between *C. maculata* and *A. aphidimyza* at different densities of *M. persicae*. The experiment was conducted at 22 ± 1°C, under a relative humidity of 70 ± 8%, and with a photoperiod of 16L:8D. The insects were placed on standardized pepper plants that were individually enclosed in a plastic cylinder (20 cm in diameter and 45 cm in height) glued to a disc platform. The top of the cylinder and the two lateral openings were covered with muslin to allow air circulation. Pepper plants used in experimental arenas had four leaves and were four weeks old. Plant apexes were cut because aphids are difficult to count when hidden in the opening terminal buds. To standardize predators, we used the same rearing and starvation conditions as in Experiment 1. At the onset of the experiment, 3rd instar aphids obtained from synchronous cohorts of *M. persicae* were transferred to the upper leaves of the plants using a fine camel-hair brush. We tested three extraguild prey densities: 10, 45, and 90 *M. persicae* per plant. These represent low, average, and high prey densities for a 3rd instar *C. maculata* larva, since Sentis *et al.* (Chapter 4) showed that *C. maculata* eats on average 35 *M. persicae* per day under the same experimental conditions. One hour after aphid introduction, one *A. aphidimyza* larva was placed near the aphid colony; 30 minutes later, a newly molted 3rd instar *C. maculata* larva was introduced at the bottom of the stem. After 24 h, the number of *M. persicae* and *A. aphidimyza* killed was recorded. We were able to distinguish aphids eaten by *C. maculata* and *A. aphidimyza* because the latter extract aphid body contents leaving a empty aphid exoskeleton (Lucas *et al.* 1998). Fifteen replicates of the IGP treatment (*M. persicae* + *A. aphidimyza* + *C. maculata*), five replicates without *C. maculata* (*M. persicae* + *A. aphidimyza*), and four replicates of the control treatment (*M. persicae* only) were tested for each aphid density. When testing model predictions, we assumed that a prediction is valid if empirical observations are within the 95% confidence interval (CI) of the model predictions. Following the law of propagation of uncertainty which is based on a first-order Taylor series expansion error, 95% CI of the model predictions were calculating using the standard errors associated with the estimates of each of the model parameters. Models were developed using R software (version 2.13.1, R Development Core Team, 2011).

Results

Experiment 1. Handling time for *A. aphidimyza* (h_{ig})

The mean (± SE) handling time for *A. aphidimyza* was 0.0032 ± 0.00034 (day prey^{-1}). This value was included in Eqs. 9, 11, 12, and 13 to generate model predictions.

Experiment 2. Testing model predictions

Only 0.5 ± 0.1% of the aphids died in the control treatment (no predator). As a result, we did not correct for natural aphid mortality in our analyses. In the treatment without the IG predator (*M. persicae* + *A. aphidimyza*), no *A. aphidimyza* larva died. In the treatment with the IG predator (*M. persicae* + *A. aphidimyza* + *C. maculata*), no *C. maculata* died and IGP was always asymmetric, with *A. aphidimyza* being killed by *C. maculata*.

As predicted by the two models, the total number of prey eaten by *C. maculata* increased with aphid density (Fig. 3). For each aphid density, predictions from the nonlinear model (Eq. 9) fit the empirical observations very well (i.e., were within the 95% CI of the predictions; Fig. 3). Predictions of both models did not differ at the low extraguild prey density (10 aphids per plant). However, the total number of prey eaten predicted by the linear model (Eq. 12) was always higher than the empirical observation, and this difference increased with aphid density (Fig. 3).

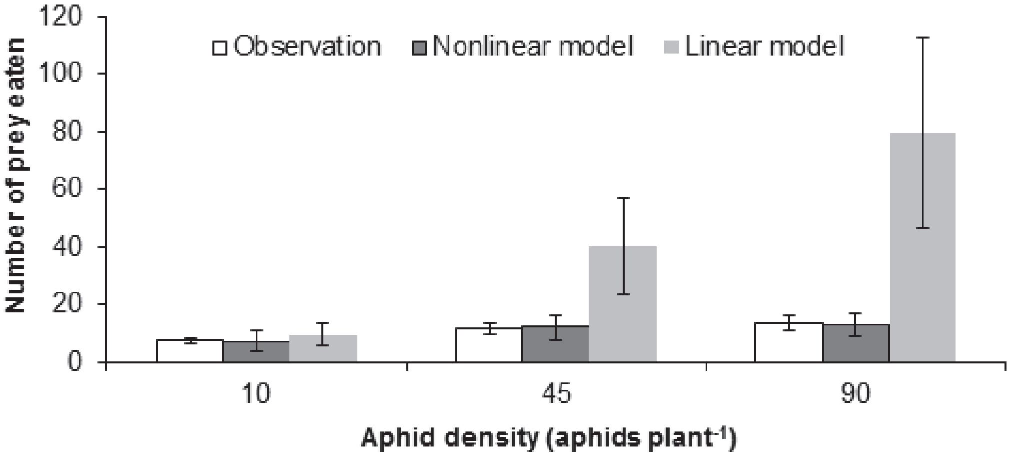

Fig. 3. Observations and predictions of the two models for the total number (± 95% CI) of prey eaten (*Myzus persicae* + *Aphidoletes aphidimyza*) by *Coleomegilla maculata* as a function of aphid density.

As predicted by the nonlinear model, the observed number of *A. aphidimyza* eaten by *C. maculata* decreased as aphid density increased (Fig. 4). Predictions from the nonlinear model (Eq. 11) fit the empirical observations well for densities of 10 and 45

M. persicae per plant, but the number of IG prey eaten at the high prey density (90 *M. persicae* per plant) is overestimated. While predictions of both models did not differ at 10 aphids per plant, the linear model prediction (Eq. 13) was higher than the empirical observation for densities of 45 and 90 aphids per plant (Fig. 4).

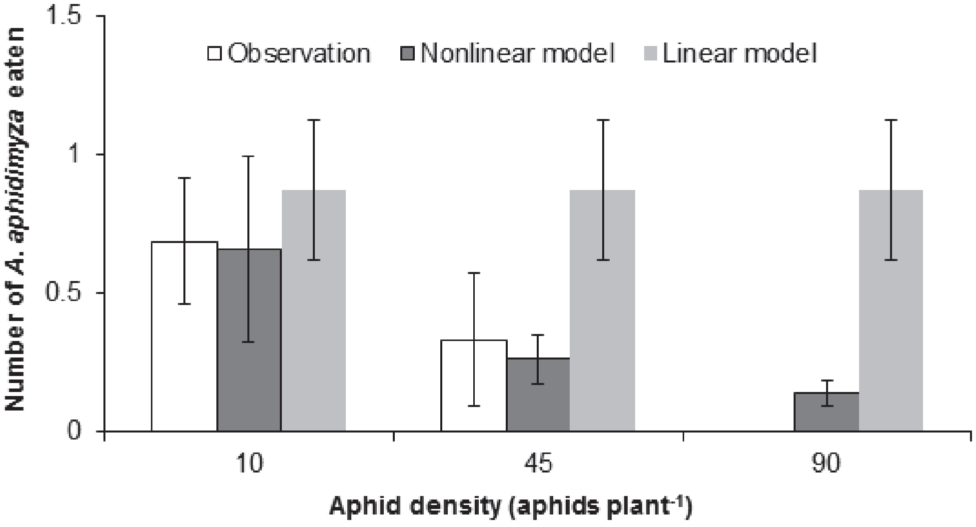

Fig. 4. Observations and predictions of the two models for the number (± 95% CI) of intraguild prey (*Aphidoletes aphidimyza*) eaten by *Coleomegilla maculata* as a function of aphid (*Myzus persicae*) density. We did not record IGP at 90 aphids plant^{-1}.

Discussion

Several models explore the conditions for coexistence of IG predators, IG prey, and EG prey (Diehl & Feissel 2000; Holt & Polis 1997; Kivan 2000; Mylius *et al.* 2001; Rudolf 2007). These models integrate different types of functional responses, mainly Holling type I and type II, but to our knowledge, no empirical study has examined which type best applies to an IG predator. In this study, we found that a model based on a linear functional response oversimplifies predator–prey interactions, resulting in predictions that largely deviate from empirical observations. In contrast, the nonlinear model fits our empirical observations well and provides a mechanistic tool that may improve our understanding of important processes underlying IG interactions and population dynamics in complex food webs.

We developed both linear and nonlinear functional response models to generate and test predictions about interacting species abundance and IGP intensity. At the low EG prey density, we observed that model predictions were similar and fit the empirical observations well, whereas only the nonlinear model fit the observations at higher EG prey densities (Figs. 3 and 4). However, the nonlinear model overestimated the number of IG prey eaten at the highest experimental EG prey density (Fig. 4). It might be that intraguild predation is too rare an event to be meaningfully analyzed when EG prey are extremely abundant.

One unrealistic assumption of the linear model is that the predator spends all its time searching for prey and eats them instantaneously, i.e., that the handling time is null. In our experiment, the good fit of the linear model at low prey density (Figs. 3 and 4) corresponds to a situation where the predator has to spend much more time searching for than handling prey. Such an assumption does not hold true when prey are abundant, thus this could explain why the linear model is not reliable at high prey densities. As a result, we conclude that the linear functional response model could be used to predict IGP interactions at high prey densities under specific and uncommon conditions, i.e., when handling or digesting times are negligible. In contrast, the nonlinear model takes into account handling time and therefore generates accurate predictions for most EG prey densities (Figs. 3 and 4). Including handling time in the model restricts predation rate at higher prey densities, as observed in our experiment (Fig. 3). Several factors influence the handling time of a predators, including predator–prey size ratio; morphological, behavioral, structural, or chemical host defenses; and predator digestive capacity (Beckerman *et al.* 2006; Brose *et al.* 2006; Jeschke *et al.* 2002). Accounting for variation in handling time values is therefore a convenient way to represent important characteristics of predator–prey interactions in models (Amarasekare 2008; Brose *et al.* 2006; Kondoh 2003; Uchida *et al.* 2007).

According to prior studies reviewed by Lucas & Rosenheim (2001), the occurrence of IGP usually decreases as extraguild prey density increases. This decrease is generally explained by a prey dilution effect (Lucas & Brodeur 2001), although the underlying mechanisms remain poorly understood (Lucas & Rosenheim 2011). An analysis of our nonlinear model and experimental results suggests that the dilution effect is linked to both handling time and EG prey density: as EG prey density increases, the time spent killing and consuming EG prey increases, which in turn reduces the time available for encountering IG prey and thereby the frequency of IGP. Therefore, variations in handling time would determine the strength of the dilution effect: the lower the handling time, the larger the number of EG prey needed for the IG prey to benefit from a dilution effect, and vice versa. As a consequence, the linear model is a poor predictor of a dilution effect because handling time is considered null.

In addition to handling time, the reliability of predator–predator models also largely depends on searching (hunting) behavior (Lucas & Rosenheim 2011; Schmitz 2007), which can be characterized by the predator search rate (Rosenheim & Corbett 2003). In functional response models, search rate determines the preference for or the ability to find a particular prey and, for a top predator, the likelihood of IGP. In our experiments, search rates for both prey were assumed similar ($a_{ig} = a_{eg}$), indicating that *C. maculata* behaved like a pure generalist (Borer *et al.* 2007; McCann & Hastings 1997). However, this might not be the case in other systems where the benefit/cost ratio of eating the IG prey varies. Lucas (2005) proposed four types of IGP: (1) opportunistic, when IGP is a fortuitous event, (2) nutritional, when nutritional benefits are associated with the eating of an IG prey, (3) competitive, when eating the IG prey eliminates an important competitor, and (4) protective, when eating the IG prey eliminates a potential predator under conditions of symmetrical IGP. In the first type, the IG predator does not explicitly search for IG prey, whereas in the three others it actively hunts IG prey because of the benefits of killing or eating them. Therefore, the type of IGP, and probably hunting strategy, are described by specific values of search rate (Lucas 2005; Rosenheim & Corbett 2003; Schmitz 2007). Accounting for search rate variations in functional response models would be a promising approach to investigate the effects of IGP type and predator searching behavior on IGP frequency, which may have important repercussions on overall food web dynamics.

Population dynamics models using a linear functional response predict that food webs that include IG interactions are unstable and not persistent, especially at higher productivity levels (Borer *et al.* 2007; Holt & Polis 1997; Holt & Huxel 2007). However, as we described above, linear functional responses do not impose limits on predation rate (Fig. 1a), which induces strong interactions at higher prey density and thus tends to be destabilizing in terms of demographic fluctuations and species coexistence (Abrams & Fung 2010; McCann *et al.* 1998). On the other hand, nonlinear functional response limits predation rate at higher prey density (Fig. 1b) and thus weakens the strength of interactions, which in turn dampens oscillations between consumers and resources, promoting community persistence and stability (Abrams & Fung 2010; McCann & Hastings 1997; McCann *et al.* 1998; Uchida *et al.* 2007). The nonlinear response model thus contributes to explaining why coexistence is possible in nature even at higher productivity levels (Abrams & Fung 2010; McCann *et al.* 1998; Rall *et al.* 2008; Uchida *et al.* 2007; Williams 2008). According to our results, and because most predators display a saturating functional response (Jeschke *et al.* 2002), IGP models should incorporate a nonlinear functional response for more realism.

To further our understanding of the nature and outcome of IGP on interacting species and the consequences for communities, empirical and theoretical studies should incorporate determinant features of animal behavior (Rosenheim & Corbett 2003; Schmitz 2007; Steffan & Snyder 2010; Williams 2008). Ours results suggest that nonlinear functional responses, through variations of search rate and handling time, add realism in population models investigating IGP. However, additional and improved data on functional response shapes and parameters under natural conditions are needed to accurately represent and parameterize this crucial model component (Williams 2008).

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Chapitre 6

Effets de la température et de la densité des proies sur la prédation intraguilde : modélisation et approche expérimentale

Cet article sera soumis à la revue *Ecology*,
Sous le titre suivant :

Effects of temperature and prey density on intraguild predation: combining modeling and experimental approaches

Arnaud Sentis, Jean-Louis Hemptinne et Jacques Brodeur

Résumé

La prédation intraguilde (IGP), c’est-à-dire la prédation entre deux compétiteurs d’espèces différentes exploitant une même ressource, est une interaction commune dans la plupart des écosystèmes naturels et aménagés. Plusieurs modèles et études expérimentales ont été développés et réalisés pour déterminer les mécanismes et les processus qui régissent les interactions intraguildes et leurs conséquences sur les dynamiques des populations et la structure des communautés. La productivité du système, caractérisée par la densité des proies extraguildes, s’est avérée un facteur clé car elle influence l’intensité de l’IGP à court terme et la coexistence des différents protagonistes à plus long terme. Un autre facteur potentiellement important est la température, car elle affecte l’ensemble des processus biologiques ainsi que la dynamique des populations, les interactions prédateur-proie et le fonctionnement des écosystèmes. Toutefois, son effet sur les interactions intraguildes reste méconnu à ce jour. Notre objectif était donc de déterminer comment la température et la productivité du système influencent le comportement du prédateur intraguilde et l’intensité de l’IGP. Nous avons d'abord développé un modèle de réponse fonctionnelle pour prédire les effets de la température et de la densité des proies sur l’IGP. Ensuite, nous avons paramétré ce modèle à partir d’observations réalisées avec un système plante-puceron-prédateur et, enfin, nous avons testé les prédictions du modèle en manipulant la température et la densité de pucerons au sein de notre système biologique. Comme prédit par le modèle, nous avons observé que la température augmente l'activité de recherche du prédateur intraguilde et, par conséquent, le taux de rencontre avec ses proies et l’intensité de l’IGP. Cependant, une augmentation de la densité des proies extraguildes amoindrit l’effet de la température en offrant une protection à la proie intraguilde par un effet de dilution. Notre étude démontre donc que l’intensité de l’IGP dépend d’un compromis entre la température et la densité des proies extraguildes. De plus, nous avons constaté que les températures basses offrent un refuge temporel à la proie intraguilde puisque l’IGP y est moins fréquente. En conséquence, nos résultats suggèrent que les variations de température et, en particulier, les températures basses contribuent à la coexistence des protagonistes engagés dans des interactions intraguildes.

Mots clés. Interactions prédateur-prédateur, productivité, théorie métabolique de l'écologie, refuge temporel, coccinelles, pucerons.

Abstract

Intraguild predation (IGP), which occurs when predators from different species compete for a common resource and feed on each other, is a very common interaction in natural and managed ecosystems. Several models have been developed and experimental studies conducted to determine the mechanisms and processes governing IG interactions and the consequences on population dynamics and community structure. System productivity, often characterized by extraguild prey density when studying IG interactions, is a key factor because it influences IGP intensity in the short term and coexistence and persistence of interacting species in the long term. Temperature also appears to play an important ecological role because it affects nearly all biological rates, population dynamics, and community structure. However, its effect on IG interactions remains unknown. In this study, our objective was to determine how temperature and system productivity influence intraguild predator behavior and IGP intensity. We first developed an IGP functional response model to predict the effects of temperature and prey densities on IGP. We next used a plant–aphid–predator mesocosm to parameterize the model. Finally, we tested the model by manipulating temperature and aphid density within our biological system. In agreement with predictions of our model, we found that warming increases predator foraging activity and encounter rate, and thus IGP intensity. However, an increase in the extraguild prey density dampened down this temperature effect by providing protection to the intraguild prey through a dilution effect. Our study thus provides evidence that temperature and extraguild prey density influence IGP intensity in opposite ways. We also found that lower temperatures provide a temporal refuge for the intraguild prey by reducing IGP. These results suggest that temperature variations, especially lower temperatures, may contribute to coexistence between interacting species in productive environments.

Key words. Predator–prey interactions, system productivity, metabolic theory of ecology, temporal refuge, ladybeetles, aphids.

Introduction

Predator diversity and multiple predator interactions greatly influence food web dynamics, community structure, and ecosystem functioning (Cardinale *et al.* 2002; Cardinale *et al.* 2006; Finke & Snyder 2010; Northfield *et al.* 2010; Sih *et al.* 1998). During the past two decades, intraguild predation (IGP), which occurs when predators belonging to different species compete for a common resource and also feed on each other (Polis *et al.* 1989), has received increasing attention given its relevance to both theoretical and applied aspects of ecology (Arim & Marquet 2004; Finke & Snyder 2010; Polis *et al.* 1989; Rosenheim 1998; Straub *et al.* 2008; Vance-Chalcraft *et al.* 2007). Several models have been developed and experimental studies conducted that were aimed at determining the mechanisms and processes governing IG interactions and the consequences on population dynamics and community structure (Borer *et al.* 2003; Borer *et al.* 2007; Mylius *et al.* 2001; Rudolf 2007; Vance-Chalcraft *et al.* 2007).

System productivity, generally characterized by extraguild prey density when studying IG interactions, is one of the key factors influencing IGP intensity in the short term (Lucas *et al.* 1998; Lucas & Rosenheim 2011) as well as the coexistence and persistence of interacting species within communities in the long term (Borer *et al.* 2003; Borer *et al.* 2007; Holt & Polis 1997). Theory predicts that only the intraguild prey persists at low productivity because it has a better capacity to exploit resources than the intraguild predator, whereas the latter should drive the IG prey to extinction at high productivity through a combination of competition and predation processes. Therefore, coexistence should only occur at intermediate levels of productivity (Borer *et al.* 2003; Borer *et al.* 2007; Diehl & Feissel 2000; Holt & Polis 1997; Mylius *et al.* 2001). However, several experiments conducted under laboratory and field conditions suggested that coexistence between predators and prey is possible over a larger gradient of productivity or extraguild prey density than expected from theory (Amarasekare 2000; Amarasekare 2007; 2008; Borer *et al.* 2003; Brodeur *et al.* 2002; Lawler & Morin 1993; Lucas & Rosenheim 2011; Morin 1999). Moreover, an increase in extraguild prey density would generally lead to a reduction in IGP intensity in the short term (reviewed by Lucas & Rosenheim 2011). Therefore, focussing on mechanisms behind the effect of system productivity may be essential to further examine how the latter influences IG interactions and community structure.

Body temperature affects enzymatic activity and thereby influences nearly all metabolic and biological rates, population dynamics, species interactions, and ecosystem functioning (Brown *et al.* 2004; Englund *et al.* 2011; Harmon *et al.* 2009; Petchey *et al.* 1999; Petchey *et al.* 2010). Despite the ecological importance of this factor, virtually nothing is known about the effect of temperature on IG interactions. For arthropod predators, rising temperature increases predator metabolism, including foraging activity, and results in higher predation rates through more frequent encounters with prey (Englund *et al.* 2011; Vasseur & McCann 2005; Zamani *et al.* 2006). In addition, the metabolic theory of ecology (MTE) suggests that (1) the Boltzmann-Arrhenius model derived from chemical reaction kinetics can be used to predict the effect of temperature on most biological rates, including predator foraging rate and handling time, and (2) the relationship between temperature and biological rates is nearly invariable and common to all organisms (i.e., universal temperature dependence hypothesis; Gillooly *et al.* 2002; Brown *et al.* 2004). Accordingly, we expect temperature to affect predator–prey and predator–predator interactions in the same way. In other words, warming should increase IGP occurrence.

Our objective was therefore to simultaneously investigate the effects of extraguild (EG) prey density and temperature as well as their interaction on IGP occurrence using both modeling and experimental approaches. In a previous study, Sentis *et al.* (Chapter 5) developed and tested a non-linear functional response model to examine the effects of extraguild prey density on predation rate of the IG predator and IGP intensity. Because this simple model fit experimental observations well (Sentis *et al.* Chapter 5), we presumed that it can be extended to include the effect of temperature on IGP. We therefore used the MTE equations for metabolic temperature dependence (Brown *et al.* 2004) to describe how temperature influences predator search rate and handling time. Next, we used a plant–aphid–predator mesocosm system to (i) parameterize the model and (ii) test its predictions by manipulating temperature and aphid density. The tri-trophic community consisted of the green peach aphid *Myzus persicae* Sulzer (Homoptera: Aphididae) as extraguild prey, the spotted ladybeetle *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae) as intraguild predator, and the predatory midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) as intraguild prey.

The model

Following the type II functional response model developed by Sentis *et al.* (Chapter 5), the total number of prey eaten by the IG predator (*C. maculata*) is:

$$N_{eg}+N_{ig}=(N_{0eg}+N_{0ig})\times(1-\frac{w(a_{eg}(h_{eg}N_{0eg}+h_{ig}N_{0ig})\times e^{-a_{eg}(t-h_{eg}N_{0eg}-h_{ig}N_{0ig})})}{a_{eg}(h_{ig}N_{0ig}+h_{eg}N_{0eg})}) \quad \textbf{(1)}$$

and the number of IG prey eaten by the IG predator is:

$$N_{ig}=N_{0ig}\times(1-\frac{w(a_{eg}(h_{eg}N_{0eg}+h_{ig}N_{0ig})\times e^{-a_{eg}(t-h_{eg}N_{0eg}-h_{ig}N_{0ig})})}{a_{eg}(h_{ig}N_{0ig}+h_{eg}N_{0eg})}) \quad \textbf{(2)}$$

where $_{eg}$ and $_{ig}$ refer to the extra- and intraguild prey, respectively. N_{eg} and N_{ig} are the numbers of EG prey and IG prey eaten by the IG predator. N_{0eg} and N_{0ig} are the initial numbers of EG prey and IG prey, ***t*** is the total experimental time, and *w* is the Lambert function (Corless *et al.* 1996). a_{eg} is the search rate (searching efficiency of the predator; units: area time^{-1}) for the EG and IG prey. h_{eg} and h_{eg} are the handling times (time to attack, kill, and eat a prey; units: time prey^{-1}) for the EG and IG prey, respectively. See Sentis *et al.* (Chapter 5) for details about the construction of these models.

Because the biochemical processes of ectotherms are largely contingent on ambient temperature (Gillooly *et al.* 2001), both search rate and handling time are a function of temperature. Based on MTE, handling time depends on body mass (*M*, in mg) and environmental temperature (*T*, in K) (Brown *et al.* 2004):

$$h(T)=h_0 M^{b_h} e^{E_h/kT} \quad \textbf{(3)}$$

where h_0 is a normalization constant independent of body size and temperature, b_h an allometric exponent, E_h the activation energy (eV; defined as the average activation energy for the rate-limiting enzymes catalyzing biochemical reactions of metabolism), and k the Boltzmann's constant (8.62×10^{-5} eV K^{-1}). The value of b_h is assumed to be 0.75, derived from the physics of distribution networks in animals (West *et al.* 1997). h_0 and E_h are estimated empirically using non-linear least square regressions. MTE predicts that energy activation ($\boldsymbol{E_h}$) is equal to 0.65 eV (Brown *et al.* 2004).

Because several authors reported a non-linear relationship between temperature and search rate (Cave & Gaylor 1989; Englund *et al.* 2011; Flinn 1991; Mack & Smilowitz

1982; Messenger 1968), we used a model accounting for non-linearity to describe this relationship (Sentis *et al.* Chapter 4):

$$a(T) = \begin{cases} 0 & \text{if } T \leq T_0 \\ b(T - T_0)(T_l - T)^{1/2} & \text{if } T_0 \leq T \leq T_l \\ 0 & \text{if } T \geq T_l \end{cases} \qquad \mathbf{(4)}$$

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.

Inserting Eqs. 3 and 4 into the model (Eqs. 1 and 2) yields the following temperature-dependent intraguild predation model:

$$N_{eg}+N_{ig}=(N_{0eg}+N_{0ig})\times(1-\frac{w(a_{eg}(T)(h_{eg}(T)N_{0eg}+h_{ig}(T)N_{0ig})\times e^{-a_{eg}(T)(t-h_{eg}(T)N_{0eg}-h_{ig}(T)N_{0ig})})}{a_{eg}(T)(h_{ig}(T)N_{0ig}+h_{eg}(T)N_{0eg})}) \quad \mathbf{(5)}$$

$$N_{ig}=N_{0ig}\times(1-\frac{w(a_{eg}(T)(h_{eg}(T)N_{0eg}+h_{ig}(T)N_{0ig})\times e^{-a_{eg}(T)(t-h_{eg}(T)N_{0eg}-h_{ig}(T)N_{0ig})})}{a_{eg}(T)(h_{ig}(T)N_{0ig}+h_{eg}(T)N_{0eg})}) \quad \mathbf{(6)}$$

Eqs. 5 and 6 represent model predictions in which the total number of prey eaten (Eq. 5) and the number of IG prey eaten (Eq. 6) are a function of temperature and both EG and IG prey densities. For simplicity, we did not develop the functions $a_{eg}(T)$, $h_{eg}(T)$, and $h_{ig}(T)$.

To generate model predictions for our experimental tri-trophic system, only three temperature functions are needed: search rate for *M. persicae* $a_{eg}(T)$, handling time for *M. persicae* $h_{eg}(T)$, and handling time for *A. aphidimyza* $h_{ig}(T)$. The first two functions, $a_{eg}(T)$ and $h_{eg}(T)$, were assessed by Sentis *et al.* (Chapter 4); the third function $\mathrm{h_{ig}(T)}$ is estimated through the experiments described below.

Materials and methods

Two experiments were designed to estimate handling time for *A. aphidimyza* as a function of temperature and to test model predictions (Eqs. 5 and 6). The experiments were conducted using insects from 2-year-old laboratory cultures. Aphids were maintained on sweet pepper plants (*Capsicum annuum* L. cv. Bell Boy) and predators were fed *ad libitum* with aphids, pollen, and a liver-based artificial diet for coccinellids

(Firlej *et al.* 2006). See Sentis *et al.* (Chapter 5) for additional information about the origin of the insects and rearing procedures. All experiments were carried out in a growth chamber (Conviron® E15) under a relative humidity of 70 ± 8%, a light intensity of 150 μmol m^{-2} s^{-1}, and a 16L:8D photoperiod. Temperature and humidity were recorded continuously using Hobo U12 (Hobo®) units.

Experiment 1: Handling time for *A. aphidimyza* as a function of temperature $h_{ig}(T)$

The first experiment was designed to estimate the handling time (h_{ig}) for *A. aphidimyza* at six temperatures (14, 18, 22, 26, 30, and 34 ± 1°C). An *A. aphidimyza* larva (1.3 mm in length) was isolated in a Petri dish (40 × 12 mm) in which a single 3rd instar *C. maculata* larva was then introduced (see Sentis *et al.* Chapter 5 for more details). An HD camera (Sony HDR-XR500©) was used to record *C. maculata* activity until it attacked a larva. We examined videos to measure the 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*. Prey size, *C. maculata* stage, and hunger (21 h of starvation) were standardized following Sentis *et al.* (Chapter 5). There were 12 replicates per temperature. Eq. 3 was next fitted to the data to describe *A. aphidimyza* handling time as a function of temperature.

Experiment 2. Testing predictions of the IGP model

This experiment aimed to record the total number of prey eaten by a *C. maculata* larva and the occurrence of IGP between *C. maculata* and *A. aphidimyza* at three *M. persicae* densities (10, 45, and 90 aphids) and three temperatures (14, 22, and 30 ± 1°C). Temperatures higher than 30°C were not tested because preliminary tests showed that they are lethal for most *A. aphidimyza* larvae (Sentis *et al.* unpublished data). Experimental arenas consisted of a plastic cylinder (20 cm in diameter and 45 cm in height) in which standardized sweet pepper plants were individually enclosed. Chosen densities of 3rd instar aphids were transferred to the upper leaves of the plants and, after 1 h of acclimatization, a 1.3 mm long *A. aphidimyza* larva was placed near the aphid colony. Thirty minutes later, a 3rd instar *C. maculata* larva was introduced into the arena (see Sentis *et al.* Chapter 5 for experimental details and standardization methods for plants, aphids, and predators). After a 24 h period, we recorded the total number of prey (*M. persicae* and *A. aphidimyza*) killed. Fifteen replicates of the IGP 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 (*M. persicae* only) were tested for each temperature–density combinations. A two-way ANOVA was used to test the effects of prey density, temperature, and their interaction on the total number of prey killed by *C. maculata*. Data were log(x+1) transformed before analyses to satisfy normality and homoscedasticity requirements. The effects of temperature, *M. persicae* density, and their interaction on the number of *A. aphidimyza* eaten by *C. maculata* were tested with a generalized linear model using a Binomial distribution and a Logit link. For each *M. persicae* density, a similar generalized model was used to test the effect of temperature on the number of *A. aphidimyza* eaten by *C. maculata*. We assumed that a model prediction is valid if the empirical observation is within the 95% confidence interval (CI) of the model prediction. Following the law of propagation of uncertainty which is based on a first-order Taylor series expansion error, 95% CI of the model predictions were calculating using the standard errors associated with the estimates of each of the model parameters. Data were analyzed using R software (v. 2.13.1, R Development Core Team, 2011).

Results

Experiment 1: Handling time for *A. aphidimyza* as a function of temperature $h_{ig}(T)$

As predicted by MTE, handling time decreases exponentially as temperature rises, and Eq. 3 adequately fits the effect of temperature on handling time for *A. aphidimyza* (Fig. 1) ($r^2 = 0.68$, $P < 0.0001$, $n = 6$). Moreover, our estimate of energy activation corresponds to the value predicted by the MTE (estimate ± SE: 0.71 ± 0.06 eV; MTE prediction: 0.65 eV).

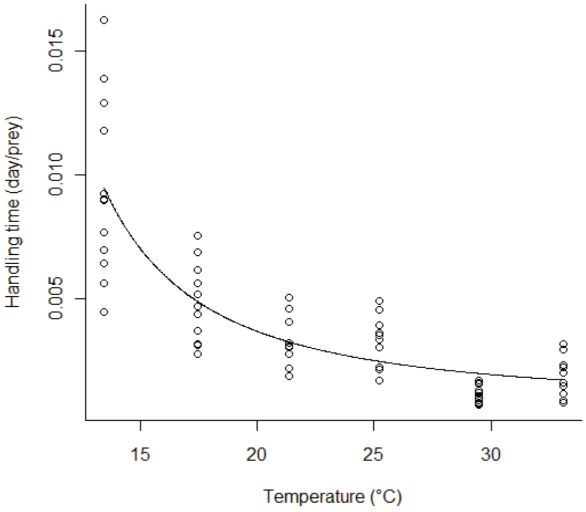

Fig. 1. Relationship between temperature and handling time for *Coleomegilla maculata* preying on *Aphidoletes aphidimyza*. $h_{ig}(T) = 3.66 \times 10^{-18} M^{0.75} e^{0.71/kT}$, where M is the predator body mass (4.71 mg), T (K) is the environmental temperature, and k is the Boltzmann's constant (8.62×10^{-5} eV K^{-1}) ($r^2 = 0.68$, $P < 0.0001$, $n = 67$).

Experiment 2. Testing predictions from the IGP model

In experiment 1, we estimated the handling time for *A. aphidimyza* as a function of temperature to be $h_{ig}(T) = 3.66 \times 10^{-18} M^{0.75} e^{0.71/kT}$. Sentis *et al.* (Chapter 4) estimated search rate and handling time for *M. persicae* as a function of temperature and found $a_{eg}(T) = 0.077\ (T\text{-}285.71)\ (309.86\text{-}T)^{1/2}$ and $h_{eg}(T) = 8.93 \times 10^{-18} M^{0.75} e^{0.9/kT}$, respectively. These three equations have been substituted into Eqs. 5 and 6 for predicting the total number of prey eaten by a *C. maculata* larva and IGP intensity. Because our primary interest was to determine the effect of temperature and EG prey density on IGP, we considered that *A. aphidimyza* density was constant ($N_{0ig} = 1$). Eq. 5 shows that the total number of prey eaten by *C. maculata* increases with both EG prey density and temperature (Fig. 2). However, predation rate decreases rapidly at high temperatures (Fig. 2). Following Eq. 6, IGP occurrence increases with temperature but decreases rapidly at high temperatures and when aphid density increases (Fig. 3).

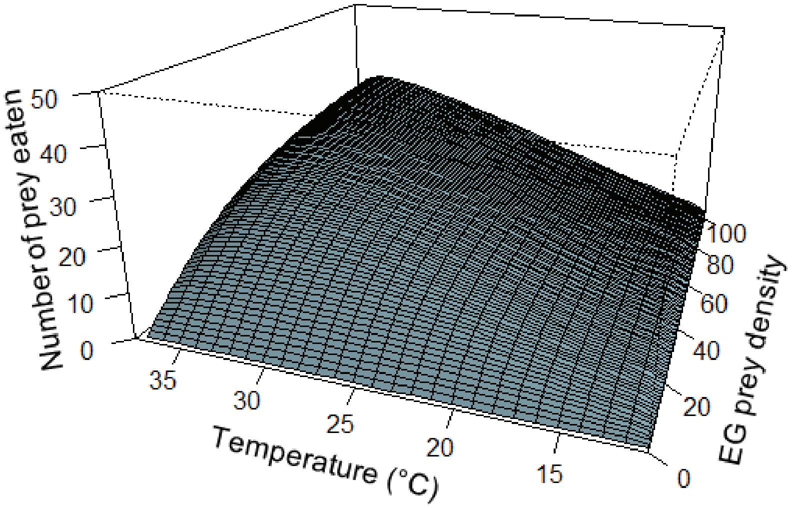

Fig. 2. Prediction of the IGP functional response model derived from Eq. 5. The total number of prey eaten is a function of temperature and extraguild (EG) prey density.

Parameters were determined using the results of Sentis *et al.* (Chapter 4) and Experiment 1. Intraguild prey density was considered to be constant ($N_{0ig} = 1$).

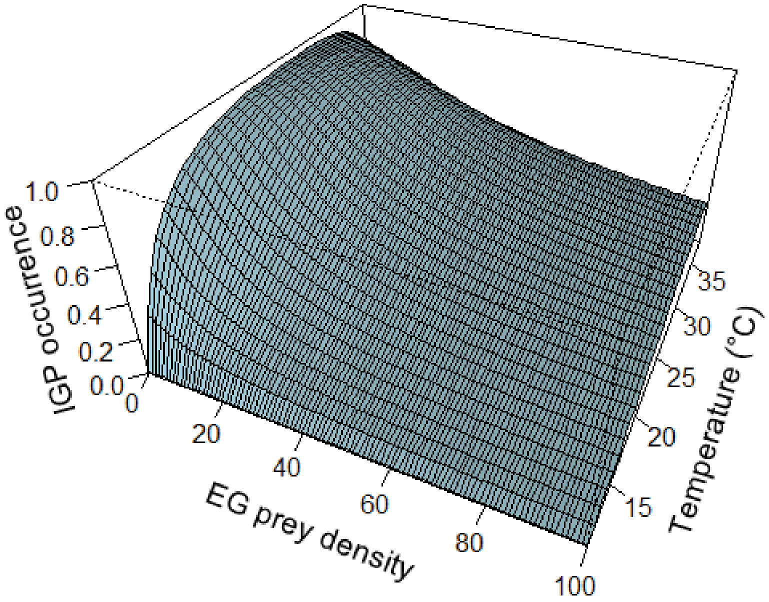

Fig. 3. Prediction of the IGP functional response model derived from Eq. 6. IGP occurrence is a function of extraguild (EG) prey density and temperature. Parameters were determined using the results of Sentis *et al.* (Chapter 4) and Experiment 1. Intraguild prey density was considered to be constant ($N_{0ig} = 1$).

Only 0.5 ± 0.1% of the aphids died in the control treatment without predator and mortality did not differ between temperatures (Wilcoxon: $\chi^2 = 8.5$, $df = 5$, $P = 0.13$). As a result, we did not correct for natural aphid mortality in our analyses. In the treatment without IG predator (*M. persicae* + *A. aphidimyza*), none of the *A. aphidimyza* larvae died. In the treatment with IG predator (*M. persicae* + *A. aphidimyza* + *C. maculata*), all *C. maculata* larvae survived and IGP was always asymmetric, with *C. maculata* being the IG predator and *A. aphidimyza* the IG prey.

As predicted by the model, the total number of prey eaten by *C. maculata* increased significantly with both aphid density and temperature (Fig. 4) [two-way ANOVA: temperature effect ($F_{2,\ 123} = 159.0438$, $P < 0.0001$), prey density ($F_{2,\ 123} = 52.05$, $P < 0.001$)], and the effect of aphid density was stronger at higher temperatures (interaction temperature × prey density: $F_{4,123} = 3.10$, $P = 0.018$). Moreover, for each aphid density–

temperature combination, the prediction (Eq. 5) fits the empirical observation, i.e., within the 95% confidence interval of the prediction (Fig. 4).

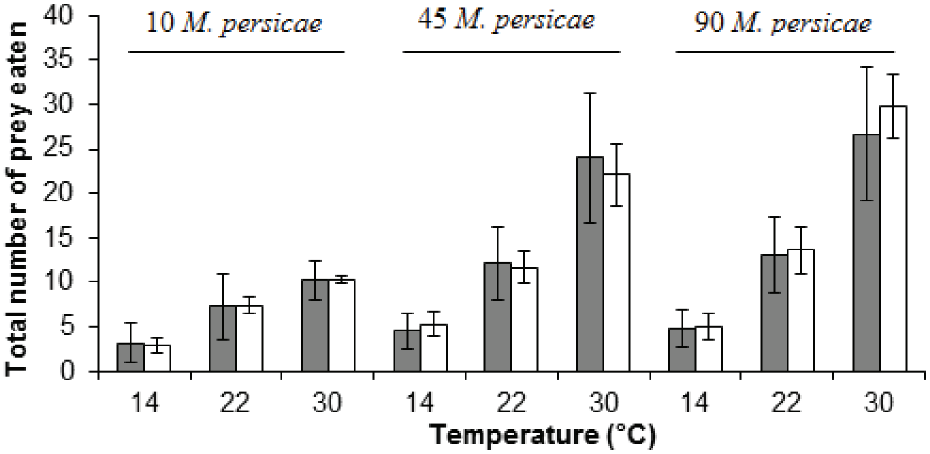

Fig. 4. Total number (± 95% CI) of prey (*M. persicae* + *A. aphidimyza*) eaten by *C. maculata* as a function of aphid density and temperature (°C). Open and solid bars represent empirical observations and model predictions (Eq. 5), respectively.

As predicted by the model, IGP was less frequent when aphid density increases (χ^2 = 32.83, *df* = 2, *P* < 0.0001, *n* = 135) and when temperature decreases (χ^2 = 43.54, *df* = 2, *P* < 0.0001, *n* = 135) (Fig. 5). The effect of temperature was similar for each aphid density treatment (interaction temperature × aphid density: χ^2 = 5.05, *df* = 4, *P* = 0.28, *n* = 135). For each *M. persicae* density, the number of *A. aphidimyza* eaten by *C. maculata* increased significantly with temperature (Fig. 5; for 10 *M. persicae*: χ^2 = 17.79, *df* = 2, *P* = 0.0001, *n* = 47; for 45 *M. persicae*: χ^2 = 14.98, *df* = 2, *P* = 0.0006, *n* = 43; for 90 *M. persicae*: χ^2 = 12.22, *df* = 2, *P* = 0.0003, *n* = 45). The prediction derived from Eq. 6 fits empirical observations well for 10 and 45 *M. persicae* (Fig. 5). However, the model overestimates IGP intensity at 22°C for high aphid density and at 14°C for medium and high aphid densities.

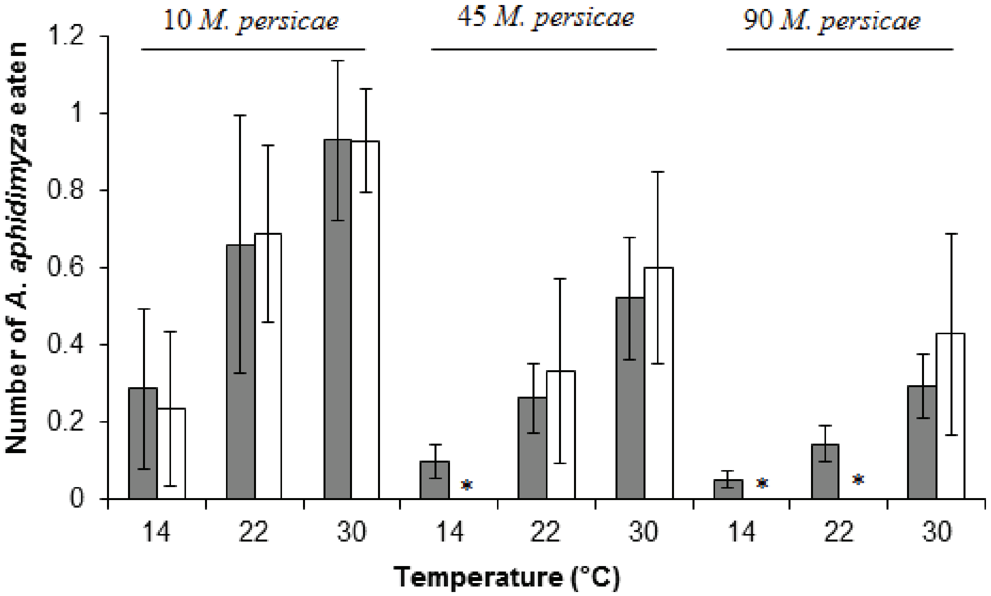

Fig. 5. Mean number (± 95% CI) of IG prey (*A. aphidimyza*) eaten as a function of temperature and aphid density. Open and solid bars represent empirical observations and model predictions (Eq. 6), respectively. Stars represent treatments for which IGP did not occur.

Discussion

Numerous studies and models have been developed to elucidate and predict IG interactions and their consequences on population dynamics and community structure (Borer *et al.* 2003; Borer *et al.* 2007; Diehl & Feissel 2000; 2001; Holt & Polis 1997; Mylius *et al.* 2001). Surprisingly, the effect of temperature—one of the most important abiotic factor influencing all organisms (Brown *et al.* 2004)—has never been investigated for IGP. In this study, we first developed a simple functional response model to predict the effect of temperature and EG prey density on predation rate of the IG predator and IGP intensity. The model predictions fit the empirical observations well (Fig. 5), except in situations where IGP is a too rare event to be meaningfully analyzed. As predicted by the model, we observed that IGP intensity depends on both temperature and EG prey density, with the two factors acting in opposite directions: IGP becomes more frequent with warming but decreases when more EG prey are available. Combining models and experiments helps us to understand the mechanisms by which temperature and EG prey density influence IG predator behavior, predation rate, and IG interactions.

Search rate and maximum predation rate (handling time^{-1}) of a predator feeding on a given prey species generally increase with temperature (Eggleston 1990; Englund *et al.* 2011; Gresens *et al.* 1982; Persson 1986; Thompson 1978; Zamani *et al.* 2006). In a previous study (Sentis *et al.* Chapter 4), we also observed that *C. maculata* larvae were more efficient at finding prey when temperature rises (expect for temperatures higher than 30°C). Based on MTE and observations of *C. maculata* larvae handling *M. persicae* (Sentis *et al.* Chapter 4), we observed that handling time for *A. aphidimyza* exponentially decreases with warming (Fig. 1). As a result, warming favours encounter and predation rates (Fig. 4) as well as IGP intensity (Fig. 5). Ours results show that, in the short term, the overall impact of temperature on predator–predator interactions is mediated by its direct effect on predator foraging activity.

For most predators, predation rate increases with prey density and reaches a maximum as described by the Holling type II functional response (Jeschke *et al.* 2002). We predicted (Eq. 5; Fig. 2) and observed a similar pattern for an IG predator (Fig. 4), indicating that the presence of an IG prey did not change the functional response of the IG predator. It is interesting to note that our model and empirical observations indicate that augmenting EG prey density decreased IGP intensity for each temperature tested, as indicated by a reduction in the number of *A. aphidimyza* eaten when prey density increased for a given temperature (Fig. 5). Following Sentis *et al.* (Chapter 5), as EG prey density increases, the time spent killing and consuming EG prey increases, thereby reducing the amount of time available for encountering the IG prey and reducing IGP intensity. However, because searching and handling rates increase with warming (Fig. 1), encounter and predation rates increase and higher numbers of EG prey are therefore needed at high temperatures to reduce IGP risk. For instance, at 30°C, IGP intensity decreased with aphid density but still occurred with 90 aphids, whereas at 14°C, we did not record IGP for treatments with 45 and 90 aphids (Fig. 5).

Our model should apply to most biological systems that include IG interactions because the effects of temperature on metabolism are similar for most organisms (Brown *et al.* 2004). However, other factors, such as spatial refuge, prey behavior or predator hunting mode, also influence IG interactions (Finke & Denno 2002; Janssen *et al.* 2007; Lucas & Brodeur 1999; Rosenheim & Corbett 2003; Rosenheim 2007; Schmitz 2007) and may modulate the temperature effect on IGP intensity. For example, Vucic-Pestic *et al.* (2011) showed that the attack rate of three carabid species increases with warming when feeding on mobile prey but is independent of temperature when feeding on slow-moving prey. Nevertheless, hunting strategies, predator and prey characteristics, and temperature responses can be mathematically represented in our model through variations in search rate and handling time which is how we modeled the functional responses (Sentis *et al.* Chapter 4, Chapter 5).

Theory predicts that, in the long term, the IG predator will drive the IG prey to extinction in highly productive environments through a combination of competition and predation processes (Borer *et al.* 2003; Borer *et al.* 2007; Diehl & Feissel 2000; Holt & Polis 1997; Mylius *et al.* 2001). However, few studies have confirmed this prediction (Diehl & Feissel 2000; 2001) and several others reported that additional mechanisms such as spatial refuge, alternative prey, intraspecific interference, or specific adaptive behavior render coexistence possible even at higher productivity levels (Finke & Denno 2002; Holt & Huxel 2007; Rudolf 2007; Uchida & Drossel 2007). Recently, Amarasekare (2007, 2008) suggested that temporal refuges, which arise from species-specific responses to abiotic environmental variations, may also promote coexistence. We observed that IGP was not frequent at the lowest temperature, thereby providing a temporal refuge to *A. aphidimyza*. Moreover, *A. aphidimyza* has a lower developmental threshold (Havelka 1980; Honěk & Kocourek 1988) and emerges earlier in the season than most of its IG predators (Bouchard & Tourneur 1981; Stewart & Walde 1997). This reinforces the scenario of *A. aphidimyza* benefiting from a temporal refuge during cold periods. Because ectotherms are highly sensitive to temperature (Brown *et al.* 2004) and have specific thermal optimum (Dixon *et al.* 2009), temporal refuges are probably more common than expected (Amarasekare 2007; Gutierrez *et al.* 2008; Hunt-Joshi *et al.* 2005; Rochat & Gutierrez 2001; Tuda *et al.* 2006), but their effects on community persistence and stability remain poorly understood (Amarasekare 2008). Integrating our model into larger population or community models would help to investigate this question.

Understanding how global warming will affect complex food webs is challenging because multiple interactions between species play an important role in the stability and resilience of ecosystems (Ives & Carpenter 2007) and in maintaining biodiversity (Bascompte *et al.* 2006). Our results suggest that predator–predator interactions will become more frequent under warmer climates, thereby modifying population dynamics and community structure. However, these interactions also depend on resource abundance at the lower trophic level. As warming increases primary productivity (Olesen & Bindi 2002), the consequence of global warming on predator–predator interactions will depend on productivity gains relative to predator response to temperature: if productivity increases faster than predator metabolism and predation rate, predator–predator interactions would be less frequent, and vice versa. Investigating this trade-off may be possible by integrating our model into a dynamic population model that represents EG prey fluctuations as a function of temperature.

Acknowledgements

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Chapitre 7

Effets de fluctuations extrêmes de température sur un système plante-herbivore-prédateur

Cet article sera soumis à la revue *Global Change Biology*,
Sous le titre suivant :

Effects of extreme temperature fluctuations on a plant–herbivore–predator system

Arnaud Sentis, Jean-Louis Hemptinne et Jacques Brodeur

Résumé

L’augmentation de la variabilité du climat et celle de la fréquence des évènements climatiques extrêmes s’avèrent deux des aspects les plus importants associés aux changements climatiques mais, jusqu’à présent, la majorité des études se sont concentrées sur les impacts de l'augmentation de la température moyenne sur les organismes et les communautés. Prédire les effets des événements climatiques extrêmes, tels que des vagues de chaleur, est un défi majeur car ils affectent non seulement les organismes mais aussi leurs interactions, ce qui complexifie largement les effets observés au niveau des communautés. Dans cette étude, nous avons exploré les conséquences de fluctuations extrêmes de température sur les organismes et leurs interactions au sein d’un système tri-trophique composé d’une plante, le poivron *Capsicum annuum*, du puceron vert du pêcher *Myzus persicae* et de la coccinelle maculée *Coleomegilla maculata*. Nos résultats démontrent que les fluctuations extrêmes de température n’avaient aucun effet sur les plantes, peu d’effets sur les larves de coccinelles et des impacts négatifs importants sur la fécondité et l’abondance des pucerons. Au niveau populationnel, les extrêmes de température diminuaient la régulation des populations de pucerons par les coccinelles mais n’influençaient pas l’impact des pucerons sur la biomasse des plants de poivrons. Enfin, la chaîne trophique étudiée était plus résistante aux températures extrêmes en présence de coccinelles qu’en leur absence; l'abondance des pucerons n'était pas influencée par les températures extrêmes en présence des coccinelles. Ce résultat suggère que les écosystèmes incluant des prédateurs qui régulent fortement les populations d’herbivores seront plus résistants aux changements climatiques que ceux sans prédateurs, lesquels sont davantage influencés par les facteurs abiotiques. Dans l'ensemble, notre étude met en évidence l'importance d'évaluer les effets des facteurs abiotiques sur chaque niveau trophique, ainsi que sur les interactions trophiques pour comprendre la réponse des écosystèmes aux changements climatiques.

Mots clés. Evènements climatiques extrêmes, interactions trophiques, stress thermique, changements climatiques, pucerons, coccinelles.

Abstract

Greater climatic variability and extreme climatic events are currently emerging as two of the most important facets of climate change, but to date most studies have examined the impacts of increasing mean temperature on organisms and communities. Predicting the effects of extreme climatic events, such as heat waves, has arisen as a major challenge because they may affect both organisms and trophic interactions leading to complex responses at the community level. In this study, we set up a simple tri-trophic system composed of a sweet pepper plant, *Capsicum annuum*; an aphid, *Myzus persicae*; and a ladybeetle, *Coleomegilla maculata* to explore the consequences of extreme temperature fluctuations on these organisms and their interactions. We found that (1) extreme temperature fluctuations affect trophic levels in specific ways with no effect on plants, significant consequences on aphids, and few effects on ladybeetles, (2) extreme temperature fluctuations decrease the impact of ladybeetles on aphid populations but do not modify the effect of aphids on plant fresh biomass, and (3) food chains including ladybeetles are more resistant to extreme temperature fluctuations than simple plant–aphid association; aphid abundance being not influenced by extreme temperatures in presence of *C. maculata*. This suggests that ecosystems with predators exerting a strong top-down control should be more resistant to extreme climatic events than ecosystems without these predators. Our study underlines the importance of assessing the effects of climatic change on each trophic level, as well as on trophic interactions to further understand aspects of the stability, resilience, and resistance of ecological communities under climatic stress.

Key words. Extreme climatic events, trophic interactions, heat stress, climactic change, aphids, ladybeetles.

Introduction

Climate shapes the abundance and distribution of species, as well as their interactions at the population and community levels (Bale *et al.* 2002; Butchart *et al.* 2010; Harrington *et al.* 2001; Parmesan 2006). Climate change has become a major concern in ecology and there are several pieces of evidence that not only higher mean temperatures but also increased climatic variability can have significant effects on organisms and ecosystems. Extremes, such as heat waves, will become more frequent and display larger amplitudes (IPCC 2007). Although their impacts are thought to be more important to many organisms than shifts in average temperatures (Easterling *et al.* 2000), most studies have focused on the effects of increasing mean temperature on organism performance without taking into account temperature variation and extreme temperatures (Bale *et al.* 2002; Brown *et al.* 2004; Harrington *et al.* 1999; Parmesan & Yohe 2003).

In contrast to change in average temperature, which is a long term process, extreme climatic events are sporadic and induce rapid changes for organisms, populations, and communities that can be measured with short term experiments (Bannerman *et al.* 2011; Ciais *et al.* 2005; De Boeck *et al.* 2010; Gillespie *et al.* 2012; Jentsch *et al.* 2007; Smith 2011). Prior studies reported that, when temperature exceeds the upper temperature threshold for growth and reproduction, organism development rate is reduced and reproduction fails (Lamb & Gerber 1985; Petavy *et al.* 2001). In the same way, Davis *et al.* (2006) reported that small fluctuations of temperature can enhance the fitness of *Myzus persicae* Sulzer (Homoptera: Aphididae). However, when fluctuations exceed the upper thermal limit for short periods, fitness decreases and populations crash. On the other hand, Davis *et al.* (2006) and Mironidis & Savopoulou-Soultani (2008) reported that animals can cope with high temperatures when they have sufficient time to recover between successive episodes of thermal stress. Together, these results suggest that organism performances decrease with the frequency and the amplitude of temperature variations or heat waves.

The outcome of climate change for a species also depends on consequential changes in the nature and strength of interactions with other organisms within the community (Tylianakis *et al.* 2008; Van der Putten *et al.* 2010; Walther 2010). In some cases, direct effects of temperature on organisms can be weaker than the indirect effects through trophic and guild interactions (Barton *et al.* 2009; Barton 2011). Understanding the effect of climatic variability on community dynamics requires knowledge of how species interact together and how these interactions are affected by temperature variation (Stenseth *et al.* 2002; Tylianakis *et al.* 2008; Van der Putten *et al.* 2010). However, studies on extreme climatic events have generally focused on a single trophic level, mainly plants (Ciais *et al.* 2005; Davison *et al.* 2010; De Boeck *et al.* 2010), and few have examined the effect on trophic interactions (Bannerman *et al.* 2011; Gillespie *et al.* 2012; Harmon *et al.* 2009; Thibault & Brown 2008). In an original study, Thibault and Brown (2008) analysed the consequences of an exceptional flood on a desert community dominated by rodents. This catastrophic event provoked species–specific mortalities, altered interspecific interactions and community species composition, resulting in a rapid and extensive reorganization of this community. The conclusion of this study is twofold. First, it suggests that the consequences of extreme climatic events on ecosystems are difficult to predict because of species–specific responses. Second, it is crucial to investigate how the effects of extreme events cascade through trophic chains to understand and predict changes in population dynamics and community structure; minor changes in trophic interactions can greatly modify community structure (Thibault & Brown 2008; Tylianakis *et al.* 2008).

Climatic disturbance can also have important consequences for the stability of communities by modifying the strength of trophic interactions (Petchey *et al.* 1999; Smith 2011; Walther *et al.* 2002). According to theory, complex ecological systems are generally more stable and resistant to invasion or climatic change than simpler ecosystems because, in complex food webs, strong, potentially destabilizing consumer–resource interactions are dampened by numerous weak interactions (McCann 2000; Petchey *et al.* 1999). For instance, Wilmers and Post (2006) showed that presence of wolves alleviate the effects of warming on carrion abundance during an El Niño phase. Resource availability for the scavenger community was a function of climatic variation before wolf reintroduction but became determined primarily by wolves after reintroduction. They concluded that ecosystems with top predators are likely to exhibit stronger biotic regulation and should be more resistant to climate change than ecosystems without top predators. Apart from this example, there is a poor understanding of the extent to which higher trophic-level interactions may increase or decrease the resistance of food webs to extreme climatic events.

Under laboratory conditions, we investigated the effects of temperature regimes, characterized by differences in the frequency and amplitude of temperature peaks, on organisms and their interactions using a plant–aphid–ladybeetle mesocosm system. Experiments were also performed to determine the effects of peak amplitude on aphid fecundity and mortality. We finally examined the role of ladybeetles for the resistance of the trophic chain to extreme temperature fluctuations.

Materials and methods

Biological system

Present and abundant in a majority of terrestrial ecosystems, aphids are contagiously distributed in time and space (Blackman & Eastop 2000). Their colonies grow rapidly and are exploited by a large guild of predator, parasitoid, and pathogen species (Blackman & Eastop 2000; Dixon 1998). Aphids and their natural enemies are sensitive to temperature changes and constitute excellent models to explore temperature effects on food-web interactions. We studied a system composed of the sweet pepper plant *Capsicum annuum* L. cv. Bell Boy, the green peach aphid *M. persicae*, and the predatory ladybeetle *Coleomegilla maculata* lengi Timberlake (Coleoptera: Coccinellidae). These species have overlapping niches and may coexist in nature or in glasshouses (Boiteau 1983).

Plant and insect production

Sweet pepper plants were grown from seed and fertilized twice a week with Nitrophoska (12-4-14) with a nitrogen concentration of 100 ppm (Plant-Prod, Montréal, Canada). Plants were used for maintenance of a colony of *M. persicae*, established from individuals collected in greenhouses from Agriculture and Agri-Food Canada, St-Jean-sur-Richelieu, Québec, Canada. About 4,000 adult *C. maculata* were collected in October 2009 in a field at Saint-Mathieu de Beloeil (45°35'N, 74°45'W, Québec, Canada), brought back to the laboratory, and reared in meshed cages (60 × 40 × 40 cm) and fed with pollen and *M. persicae.* All insects and plants were reared in growth chambers (Conviron® E15) at 24 ± 1°C, 50–60% relative humidity, 150 µmol m^{-2} s^{-1} light intensity, and under a 16L:8D photoperiod.

Experimental design

Two experiments were conducted in 2010 under a relative humidity of 70 ± 9% and a photoperiod of 16L:8D. Four week old pepper plants having four unfurled leaves were individually placed into plastic cylinders (ø: 20 cm; h: 45 cm) glued to a plastic disc platform. The top of the cylinder and the two lateral openings were covered with mesh muslin for ventilation. Adult *M. persicae* used in all experiments were obtained from synchronous cohorts. During the experiments, temperature and humidity were recorded continuously using Hobo U12 (Hobo®) units.

Experiment 1. Effects of temperature peaks on the tri-trophic system

A factorial experiment was set up to measure the effect of five fluctuating temperature regimes on plants, aphids, and coccinellids. The temperature regimes were: (1) constant temperature of 23°C, (2) one peak of 30°C every day, (3) one peak of 30°C twice a week, (4) one peak of 40°C every day, and (5) one peak of 40°C twice a week (Fig. 1). Each temperature regime was designed so that the average temperature over the entire experimental period was 23°C. In regimes 3 and 5, temperature was averaged to 23°C on days with a peak, and kept constant at 23°C on days without a peak. These temperature regimes mimic summer conditions in southern Québec (Environment Canada 2010).

The three experimental trophic level treatments were: (1) *Plant treatment* (*C. annuum* only), (2) *Aphid treatment* (*C. annuum* + *M. persicae*), and (3) *Predator treatment* (*C. annuum* + *M. persicae* + *C. maculata*). During the experiment, pepper plants were fertilised every three days with 100 ml water containing Nitrophoska (12-4-14). At the onset of the experiment, four adult *M. persicae* were transferred to the upper leaves of each plant using a fine camel hair brush. In the *Predator treatment*, aphids were left 24 h to acclimatize and then a newly hatched 1st instar *C. maculata* larva was introduced near the aphid colony. After 10 days, the number of aphids per plant and plant fresh biomass (except roots) were recorded. *C. maculata* larvae were isolated in Petri dishes (ø 90 mm) at 23°C, starved for 24 h, and then weighed using a micro-balance (Mettler Toledo MT5). After weighing, they were fed *ad libitum* with *M. persicae* and their developmental time from eclosion to pupation was recorded.

Two controlled-temperature growth chambers were available to run the experiment and we proceeded as follows. At the beginning of the experiment, two temperature regimes were randomly selected and each assigned to a growth chamber. As each temperature regime was repeated twice, we therefore not chose the same regime for a given period. Each growth chamber contained 18 cylinders and was divided in three blocks of six cylinders to control potential environmental heterogeneity within growth chambers. For the first repetition of each temperature regime, two blocks had 1 *Plant treatment*, 3 *Aphid treatments*, and 2 *Predator treatments*. The other block consisted of 1 *Plant treatment*, 2 *Aphid treatments*, and 3 *Predator treatments*. For the second repetition, two blocks had 1 *Plant treatment*, 2 *Aphid treatments*, and 3 *Predator treatments*. The remaining block consisted of 1 *Plant treatment*, 3 *Aphid treatments*, and 2 *Predator treatments*. As a result, for each temperature regime, the experiment was repeated fifteen times for the *Predator treatment* and *Aphid treatment* and six times for the *Plant treatment*.

Mixed model ANOVAs with blocks and dates as random factors nested within temperature regimes were used to test the effects of trophic level treatments (*Plant treatment, Aphid treatment*, and *Predator treatment*), temperature regimes, and their interaction on plant biomass and aphid abundance. When temperature regimes or interactions with temperature regimes had a significant effect on the dependent variable, mixed model ANOVAs were used to investigate the effects of trophic level treatments, temperature peak amplitude, peak frequency, and their interactions. Post-hoc Tukey tests were used to test for differences between means. The effects of temperature regimes on *C. maculata* larval weight and developmental time were analyzed with one-way ANOVAs while the effects of peak frequency, peak amplitude, and their interaction were analyzed with two-way ANOVAs.

Experiment 2. Effect of temperature peak amplitude on aphid fecundity and new born aphid mortality

To examine the effect of temperature peak amplitude on aphid fecundity, four adult *M. persicae* were transferred into a cylinder containing a pot with a sweet pepper plant (see above). A treatment with 15 new born (less than 24 h old) aphids per plant was also conducted to assess their mortality. Experimental units were exposed to three temperature regimes for 24 h: (1) constant 23°C, (2) one 30°C peak, and (3) one 40°C peak. All regimes had an overall average of 23°C and the peaks were similar to those of regimes 3 and 5 from the first experiment (Figs. 1a and 1c). For each temperature regime, there were 26 replicates with adult aphids and 10 replicates with new born aphids. After 24 h, the number of aphids per plant was recorded. ANOVAs were used to test the effects of temperature regimes on adult fecundity and new born aphid mortality. Data were log(x+1) transformed before analyses to satisfy normality and homoscedasticity requirements. All data were analyzed using JMP v.8. (SAS Institute 2008).

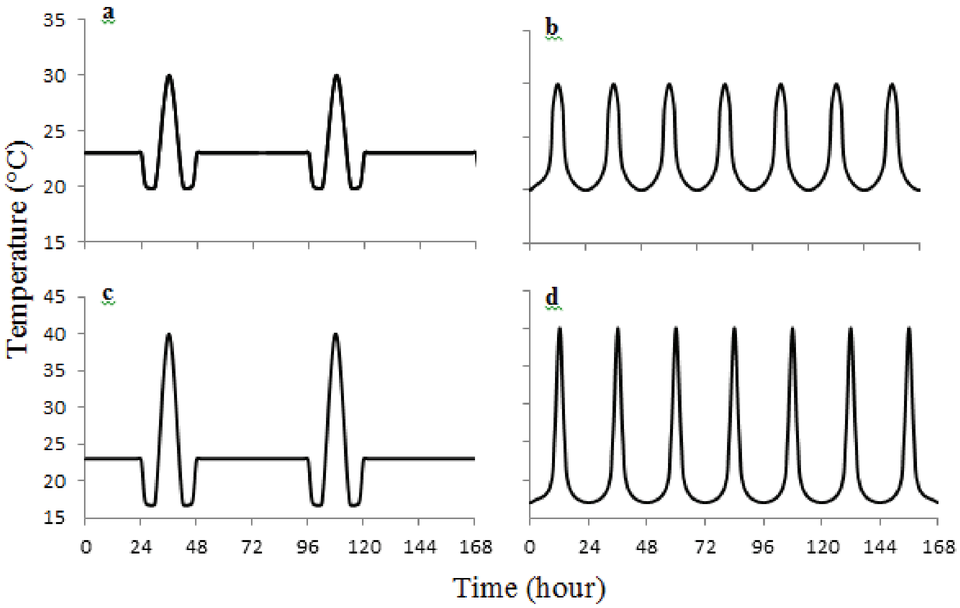

Fig. 1. The four regimes in which temperature varied: **(a)** one peak of 30°C twice a week, **(b)** one peak of 30°C every day, **(c)** one peak of 40°C twice a week, and **(d)** one peak of 40°C every day.

Results

Experiment 1. Effects of temperature peaks on the tri-trophic system

<u>Plant fresh biomass</u>

Plant biomass was not effected by temperature regime ($F_{4,\ 5.25} = 0.96$, $P = 0.50$), but was significantly reduced by trophic level treatments (Fig. 2; $F_{2,\ 10.94} = 18.19$, $P = 0.0003$). The effect of aphid on plant fresh biomass was similar with and without *C. maculata* (Fig. 2) and across temperature regimes (temperature regimes × trophic level treatments; $F_{8,\ 10.61} = 0.76$, $P = 0.64$).

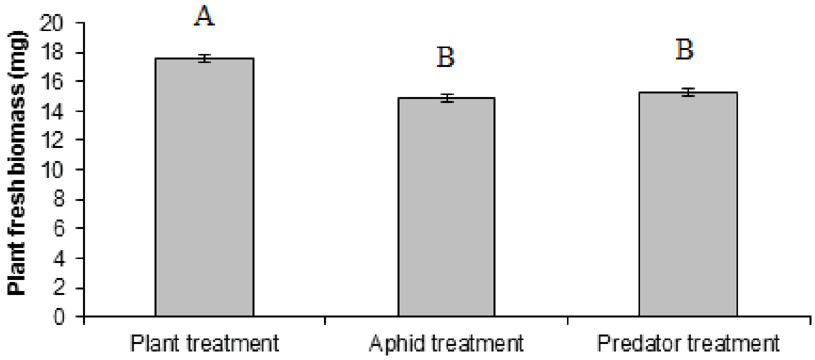

Fig. 2. Mean fresh biomass (± SE) of sweet pepper plants in the three trophic level treatments. Histograms topped by different letters are significantly different ($P < 0.05$).

Aphid abundance

Aphid abundance differed between temperature regimes ($F_{4,\ 4.97} = 8.62$, $P = 0.018$; Fig. 3) and the *Predator treatment* significantly decreased aphid abundance ($F_{1,\ 5.39} = 799.14$, $P < 0.0001$; Fig. 3), but this effect varied with temperature regime (temperature regimes × trophic level treatments $F_{4,\ 5.26} = 48.89$, $P = 0.0002$; Fig. 3). In the *Aphid treatment*, *M. persicae* abundance was significantly lower when temperature peaks were more frequent and with larger amplitude whereas in the *Predator treatment*, aphid number did not differ among temperature regimes (Fig. 3).

High amplitude peaks decreased aphid abundance ($F_{1,\ 3.98} = 18.36$, $P = 0.013$; Fig. 3). However, aphid abundance was not influenced by temperature peak frequency ($F_{1,\ 3.98} = 4.76$, $P = 0.09$) or interaction between peak amplitude and frequency ($F_{4,\ 3.98} = 0.01$, $P = 0.94$). Increasing peak frequency or amplitude reduced the impact of ladybeetle larvae on aphid abundance (trophic level treatments × peak amplitude $F_{1,\ 5.9} = 129.84$, $P < 0.0001$; trophic level treatments × peak frequency $F_{1,\ 5.76} = 53.20$, $P = 0.0004$; Fig. 3). As these interactions were significant, we tested the effects of peak frequency and amplitude for each trophic level. In the *Predator treatment*, aphid abundance was not affected by peak frequency ($F_{1,\ 3.95} = 1.06$, $P = 0.36$), amplitude ($F_{1,\ 3.95} = 7.37$, $P = 0.054$), or their interaction ($F_{1,\ 3.95} = 0.04$, $P = 0.85$). In contrast, in the *Aphid treatment*, aphid abundance decreased with peak amplitude ($F_{1,\ 3.99} = 33.33$, $P = 0.0045$) and frequency ($F_{1, 3.99} = 9.67$, $P = 0.036$), but was not affected by their interaction ($F_{1, 3.99} = 0.0052$, $P = 0.95$).

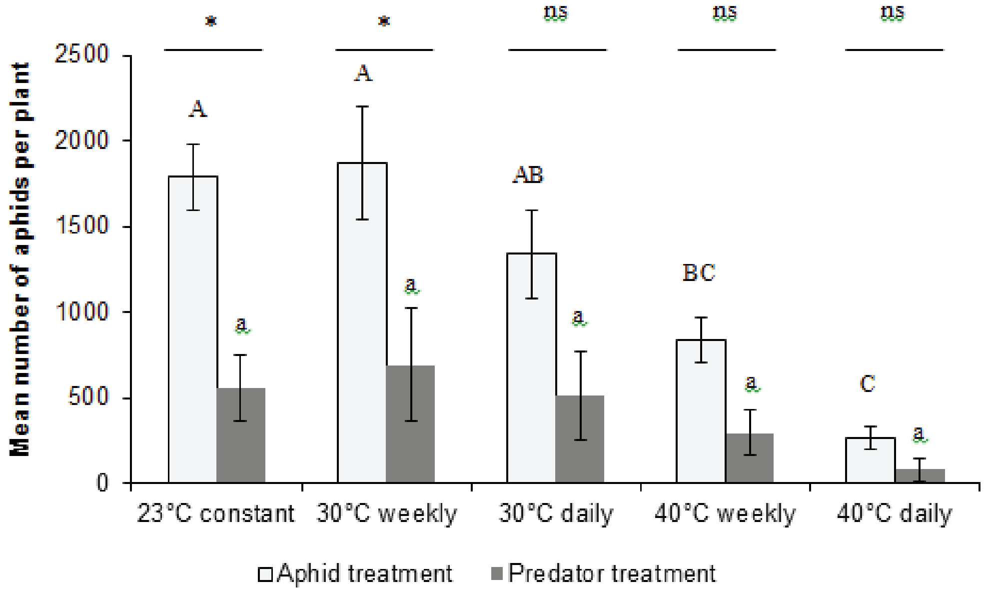

Fig. 3. Mean number per plant (± SE) of *Myzus persicae* in the five temperature regimes for the *Aphid* and *Predator treatments*. Within *Predator treatment* and *Aphid treatment*, bars topped by different small or capital letters, respectively, are significantly different ($P < 0.05$). Within temperature regimes, "ns" stands for not significant and * indicates significant differences ($P < 0.05$) between *Predator treatment* and *Aphid treatment*.

<u>*C. maculata* developmental time and larval weight</u>

Temperature regimes affected *C. maculata* larval weight ($F_{4, 54} = 5.69$, $P = 0.0007$; Fig. 4), which was reduced by both peak amplitude ($F_{1, 42} = 12.65$, $P = 0.0009$) and frequency ($F_{1, 42} = 16.47$, $P = 0.0128$). There was no interaction between peak frequency and amplitude ($F_{1, 42} = 2.89$, $P = 0.0965$).

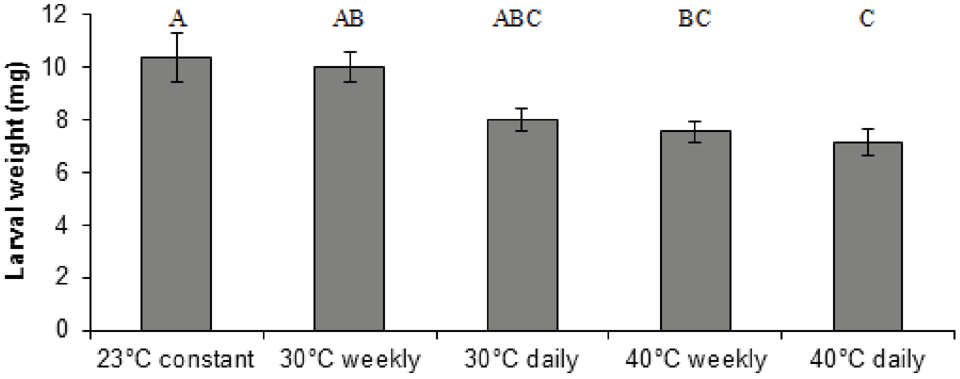

Fig. 4. Effect of the five temperature regimes on *Coleomegilla maculata* mean larval weight (± SE). Bars topped by different letters are significantly different ($P < 0.05$).

Temperature regimes affected *C. maculata* larval developmental time ($F_{4,\,54} = 4.34$, $P = 0.0041$; Fig. 5), which was longer for larvae exposed to 40°C peaks compared to 30°C peaks (peak amplitude: $F_{1,\,42} = 6.65$, $P = 0.0135$). Larval developmental time was not affected by peak frequency ($F_{1,\,42} = 0.57$, $P = 0.45$) or by the interaction between peak frequency and amplitude ($F_{1,\,42} = 0.37$, $P = 0.54$).

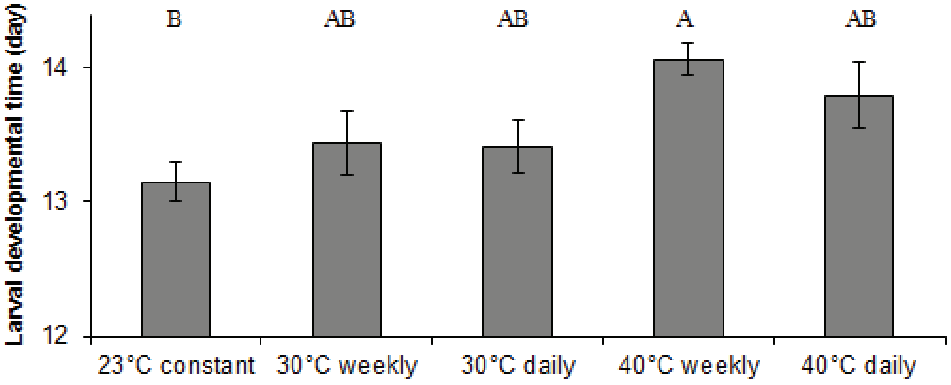

Fig. 5. Effect of the five temperature regimes on *Coleomegilla maculata* mean larval developmental time (± SE). Bars topped by different letters are significantly different ($P < 0.05$).

Experiment 2. Effect of temperature peak amplitude on aphid fecundity and new born aphid mortality

The mortality of new born aphids was very low (1.12%) and did not differ among temperature regimes ($F_{2,\ 22} = 0.0002$, $P = 0.99$); we therefore did not correct for mortality in the fecundity experiment. Adult aphids experiencing a peak of 30°C or 40°C were significantly less fecund than individuals maintained at 23°C ($F_{2,\ 67} = 16.15$, $P < 0.0001$; Fig. 6).

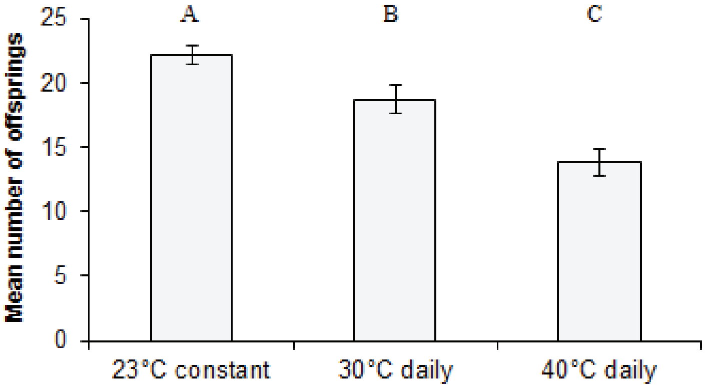

Fig. 6. Effect of three temperature regimes on *Myzus persicae* fecundity (± SE). Bars topped by different letters are significantly different ($P < 0.05$).

Discussion

The frequency and amplitude of extreme climatic events are predicted to increase with global warming and have greater impacts on ecosystems than increasing mean temperatures (Easterling *et al.* 2000). However, few studies have investigated the effects of extreme climatic events on organisms, trophic interactions, and food web dynamics (Bannerman *et al.* 2011; Harmon *et al.* 2009; Thibault & Brown 2008). Using a simple plant–herbivore–predator system we explored the consequences of temperature regimes, that differed in the frequency and amplitude of thermal peaks but not in average temperature, on both organisms and their interactions. We observed that (1) extreme temperature fluctuations affect trophic levels in specific ways with no effect on plants, significant consequences for aphids, and few effects on ladybeetles, (2) extreme temperature fluctuations decrease the impacts of ladybeetles on aphid populations but do not modify the effects of aphids on plant fresh biomass, and (3) food chains including ladybeetles are more resistant to extreme temperature fluctuations than simple plant–aphid association. Our study underlines the importance of assessing the effects of climatic change on each trophic level, as well as on trophic interactions to further understand aspects of the stability, resilience, and resistance of ecological communities under climatic stress.

Effects of extreme temperature fluctuations on organisms

Previous studies reported that heat waves generally decrease plant performance in nature because they are often associated with water stress, which can be more important than the direct effect of temperature (Ciais *et al.* 2005; De Boeck *et al.* 2010; Mittler 2006; Porter & Semenov 2005). In our experiment, water was not a limiting factor and temperature variations were similar to those experienced by pepper plants in nature (Environment Canada 2010). Moreover, the sweet pepper cultivar used (Bell Boy) has been selected for green house production where temperatures are highly variable. This probably explains the lack of plant responses to temperature peaks in our study.

Agricultural pest insects are predicted to be more abundant with climatic change because increasing mean temperature generally enhances insect fecundity and developmental rate (Bale *et al.* 2002; Cannon 1998; Newman 2006). In contrast with this prediction, we observed that aphid populations were strongly reduced by extreme temperatures (Fig. 3). In a 24 h experiment, temperature peaks of 30°C or 40°C did not affect *M. persicae* mortality but decreased its fecundity (Fig. 6), which probably explains the reduction observed in the former experiment. Other studies also reported that aphids may produce less offspring, suffer from developmental damage, and lose their beneficial endosymbiosis under extreme temperatures (Bensadia *et al.* 2006; Davis *et al.* 2006; Hazell *et al.* 2010). In contrast with predictions based on mean temperature increase, we therefore hypothesize that extreme weather events associated with climatic change would lead to a reduction of aphid populations.

The few studies investigating the effects of extreme high temperatures on natural enemies have reported contradicting results. The parasitoid *Aphidius avenae* Haliday (Hymenoptera: Braconidae) is less fecund when exposed to high temperatures (Roux *et al.* 2010), while *Aphidius matricariae* Haliday (Hymenoptera: Aphidiidae) foraging ability and fecundity were not affected by similar temperature regimes (Bannerman *et al.* 2011). In our study, extreme temperatures lead to a reduction in *C. maculata* larval weight and an increase in developmental time (Figs. 4 and 5). As ladybeetle weight is positively correlated with fecundity (Stewart *et al.* 1991), our results suggest that extreme temperature fluctuations can decrease ladybeetle fitness and thereby lower their abundance in the long term.

Plants, herbivores, and predators were differentially affected by extreme temperatures with a large impact on aphid populations, a moderate impact on ladybeetle larvae, and no effect on plant biomass (Figs. 2, 3, 4, and 5). The relative sensitivity of each trophic level to temperature changes suggests that communities are unlikely to respond as an uniform entity to climatic change as is sometimes assumed (Schmitz *et al.* 2003). Over the long term, extreme temperatures are likely to disrupt trophic relationships between organisms resulting in important changes in population dynamics and communities. However, given the stochastic nature of extreme climatic events, their frequency, amplitude, and duration are highly variable (De Boeck *et al.* 2010). As illustrated by our results, when heat waves were less frequent or of smaller amplitude, we observed few effects on organisms and few or any modifications in the dynamics of our simple tri-trophic system. We conclude that the effects of extreme climatic events on organisms and communities largely depend on their frequency and amplitude.

Effects of extreme temperature fluctuations on trophic interactions

M. persicae significantly decreased sweet pepper biomass independently of temperature regime and *C. maculata* presence (Fig. 2). As aphid damage to plants (excluding virus transmission) is relative to their abundance (Dixon 1998), which decreased with extreme temperatures and predators, we would expect a relationship between temperature regime, predation by *C. maculata* and plant biomass reduction. Our experiment was likely too short to reveal benefits that pepper plants may gain from a reduction in aphid abundance.

Extreme temperature fluctuations had a major effect on the strength of tye predator–prey interaction. *Coleomegilla maculata* significantly decreased aphid abundance but this effect was weakened by both the amplitude and frequency of temperature peaks (Fig. 3). As a result, in three temperature regimes (30°C daily, 40°C weekly, and 40°C daily), aphid abundance did not differ with and without *C. maculata* (Fig. 3). These results challenge those of models and studies based on mean temperature that predict an increase in the strength of top-down control with climate change (Barton *et al.* 2009; Rall *et al.* 2010; Vucic-Pestic *et al.* 2011). According to Sentis *et al.* (Chapter 4), the strength of a predator–prey interaction increases with warming, reachs an optimum, and then decreases at higher temperatures. As prior models and studies generally did not take into account high temperatures, a part of the relationship between temperature and interaction strength is missing. This suggests that extreme climatic events have to be taken into account in order to predict the effects of climate change on trophic interactions and community dynamics as they can differ from those observed for shifts in average temperature.

Effects of ladybeetle on food web resistance to extreme temperature fluctuations

The relationship between biodiversity and the resistance of natural communities to disturbance has emerged as an important ecological question, but few studies have investigated this issue in the context of climate change. Prior results suggest that higher trophic interactions and top-predators play an important role in the resistance of food web to disturbance (Harmon *et al.* 2009; McCann 2000; Wilmers & Post 2006). We observed that extreme temperatures led to a decrease in aphid populations only when *C. maculata* was absent (Fig. 3). In other words, ladybeetles buffer the direct effects of extreme temperatures on aphid populations. In the absence of temperature variation, aphids had the highest fecundity but ladybeetles have also the strongest impact on aphid abundance. As the severity of the temperature regime increased, aphid fecundity decreased but ladybeetles have also had a lower impact on aphid abundance. As a result, in the presence of *C. maculata*, aphid populations did not vary as a function of temperature regime. In a scenario without predators, aphid populations would fluctuate in response to temperature variation while, in presence of predators, aphid populations would be more stable. As reported by Wilmers and Post (2006), our results suggest that ecosystems with predators exerting an important biotic control of prey populations should be more resistant to climate change than ecosystems lacking them. Therefore, if the objective is to conserve communities and ecosystem functions on which we are dependent, these predators should be protected to minimize the influence of climatic change on ecological communities.

Conclusion

In natural systems, food webs are generally complex, involving many species that interact with each other in direct and indirect ways. It is therefore difficult to identify general patterns for the influence of climate change on trophic interactions and community dynamics (Petchey *et al.* 1999; Van der Putten *et al.* 2010; Walther 2010). As for most laboratory studies, our small-scale, short-term experiments were conducted in an artificial environment that has little in common with natural conditions. However, our approach remains useful to determine mechanisms and processes behind the observed responses of species and communities to temperature extremes, as this would not be possible in nature given the stochastic nature of extreme weather events. To conclude, the effects of extreme climatic events on organisms, populations, and communities are difficult to predict because (1) each species has its own sensitivity to thermal stress, (2) the effects of extreme temperature fluctuations depend on their frequency and amplitude which are highly variable in nature, (3) the response of communities depends not only on the sensitivity of individual species to environmental changes but also on trophic and guild interactions.

Acknowledgements

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Chapitre 8

Discussion et conclusion générale

1. Rappel de la problématique et présentation des principaux résultats

Comprendre quels sont et seront les effets des changements climatiques sur les écosystèmes représente un défi majeur étant donné la complexité du fonctionnement de ces derniers et la multitude de facteurs abiotiques associés aux perturbations climatiques. Ces facteurs qui sont la température, l'humidité, les précipitations, la concentration en CO_2 et les radiations solaires sont tous susceptibles d'influencer les organismes mais c'est certainement la température qui a le plus d'impact sur l'histoire de vie des organismes ectothermes (Parmesan 2006; Porter *et al.* 1991; Stacey 2003). De par son effet sur leur métabolisme, la température influence la quasi-totalité des processus biologiques avec des répercussions au niveau de la dynamique des populations et de la structure des communautés (Brown *et al.* 2004; Gillooly *et al.* 2001; Petchey *et al.* 1999; Petchey *et al.* 2010). Ainsi, lorsque la température s'accroît, on observe généralement une augmentation du taux d'accroissement des populations et du nombre de générations par année en raison d'une saison de croissance plus longue et plus chaude (Parmesan & Yohe 2003; Parmesan 2006)

Bien que l'effet de la température sur les organismes soit relativement bien connus, ses conséquences sur les interactions trophiques le sont beaucoup moins (Tylianakis *et al.* 2008). Dans les communautés naturelles ou aménagées, chaque espèce interagit avec un grand nombre d'autres espèces, que ce soit d'un même niveau trophique ou d'un niveau différent. Il est donc essentiel d'examiner ces interactions afin de mieux comprendre et prédire quel seront les effets des changements climatiques sur les populations, les communautés et les écosystèmes (Tylianakis *et al.* 2008; Van der Putten *et al.* 2010). Plusieurs études ont documenté l'effet de la température sur les interactions plante-herbivore mais peu se sont intéressées aux interactions multitrophiques, telles que les interactions plante-herbivore-prédateur ou proie-prédateur-prédateur qui sont pourtant communes dans tous les écosystèmes terrestres et aquatiques (Arim & Marquet 2004; Van der Putten *et al.* 2010).

Selon le dernier rapport de l'*Intergovernmental panel on climatic change* (IPCC 2007), les changements climatiques seront non seulement caractérisés par une hausse générale des températures mais aussi par une augmentation de la variabilité de la température et de la fréquence des extrêmes thermiques. De manière générale, les températures extrêmes ont des effets négatifs sur les organismes et réduisent le taux intrinsèque d'accroissement de leurs populations (Davis *et al.* 2006; Mironidis & Savopoulou-Soultani 2008; Morgan *et al.* 2007; Wang & Tsai 2007; Yocum *et al.* 1991). Néanmoins, la plupart des études réalisées jusqu'à présent se concentrent sur un seul niveau trophique et ne tiennent pas compte des interactions avec les autres niveaux trophiques qui peuvent largement modifier l'impact des températures extrêmes sur la dynamique de la chaîne alimentaire (Bannerman *et al.* 2011; Wilmers & Post 2006).

Ce projet visait donc à déterminer l'effet de la température et de ses variations sur un modèle biologique à trois niveaux trophiques composé d'une plante hôte, le poivron *Capsicum annuum* L. (Solanales : Solanaceae), d'un herbivore, le puceron vert du pêcher *Myzus persicae* Sulzer (Homoptera : Aphididae), ainsi que de deux de ses ennemis naturels : la coccinelle maculée *Coleomegilla maculata lengi* Timberlake (Coleoptera : Coccinellidae) et la cécidomyie prédatrice *Aphidoletes aphidimyza* Rondani (Diptera : Cecidomyiidae). L'utilisation conjointe de modèles et d'expériences nous a permis de mieux comprendre et prédire l'effet de la température sur le système étudié. Les principaux objectifs étaient les suivants : (1) développer un modèle qui prédit l'effet de la température sur le comportement, le taux de prédation et l'efficacité énergétique d'un prédateur aphidiphage en fonction de la densité de ses proies **(Chapitre 4)**, (2) développer, tester et valider un modèle qui prédit l'intensité de la prédation intraguilde en fonction de la densité de proies extra- et intraguildes **(Chapitre 5)**, (3) inclure l'effet de la température dans le précédent modèle et tester les prédictions qui en découlent à l'aide de notre système biologique **(Chapitre 6)**, (4) déterminer les effets de fluctuations extrêmes de température sur les organismes étudiés, leurs interactions et la dynamique de la chaîne trophique étudiée **(Chapitre 7)**.

La réponse fonctionnelle est une composante essentielle des modèles prédateur-proie puisque son type (I, II ou III) influence considérablement l'impact des prédateurs sur les populations de proies (Abrams & Fung 2010; McCann *et al.* 1998). C'est pourquoi les travaux de modélisation effectués dans cette thèse se concentrent essentiellement sur la réponse fonctionnelle des prédateurs. En premier lieu, nous avons développé un modèle de réponse fonctionnelle dépendant de la température **(Chapitre 4).** Pour cela, nous avons utilisé les équations du *Metabolic Theory of Ecology* (MTE) (Brown *et al.* 2004) pour modéliser l'effet de la température sur les deux paramètres de la réponse fonctionnelle : le temps de manipulation et l'efficacité de recherche du prédateur. Par la suite, ce modèle général fut appliqué au système biologique étudié et des expériences en chambres de croissance ont permis de tester les prédictions qui en découlent. Conformément aux études précédentes (Jalali *et al.* 2010b; Mack & Smilowitz 1982; Zamani *et al.* 2007) et aux prédictions du MTE (Brown 2004), nous avons observé que, lorsque la température augmente, *C. maculata* est plus efficace pour trouver et manipuler ses proies, ce qui se traduit par un taux de prédation plus élevé. En revanche, contrairement aux prédictions du MTE, à haute température, l'efficacité de recherche de *C. maculata* décroît, ce qui diminue le taux de prédation. L'activité de prédation est donc limitée à une fenêtre thermique en dehors de laquelle elle est réduite ou nulle. Un grand nombre d'études ont démontré l'existence et l'importance de cette fenêtre thermique pour la survie, le développement et la fécondité des organismes (Briere *et al.* 1999; Dixon *et al.* 2005; Dixon *et al.* 2009; Honĕk & Kocourek 1988) mais très peu d'études ont établi un lien entre celle-ci, le métabolisme des prédateurs, leurs comportements et le taux de prédation (Pörtner *et al.* 2006; Pörtner & Farrell 2008). Notre étude est donc l'une des premières dans ce sens et démontre l'importance de considérer cette fenêtre thermique pour mieux comprendre les effets de la température sur les interactions prédateur-proie. Cet aspect est particulièrement important car ces effets se répercutent au niveau des populations (Vasseur & McCann 2005) et des communautés (Petchey *et al.* 2010).

L'efficacité énergétique d'un organisme, c'est-à-dire l'énergie ingérée par rapport aux dépenses énergétiques du métabolisme de base, détermine la quantité d'énergie disponible pour sa croissance et reproduction (Vucic-Pestic *et al.* 2011). Par conséquent, cette variable détermine en partie l'aptitude phénotypique ou « *fitness* » des organismes et influence la dynamique des populations et la stabilité des communautés (Vasseur & McCann 2005). Il n'existe pas de consensus quant à l'effet de la température sur l'efficacité énergétique des prédateurs; certaines études ont rapporté qu'elle augmente avec la température (Vasseur & McCann 2005) tandis que d'autres ont observé la relation inverse (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011). En considérant une large gamme de températures, nous avons trouvé que l'efficacité énergétique de la coccinelle maculée augmente avec la température, atteint un maximum puis diminue lorsque la température continue de s'accroître. Cette observation permet donc d'expliquer la divergence des résultats précédents : le sens de la pente de cette relation dépend de la gamme de température considérée. Notre étude souligne donc la nécessité d'inclure le concept de fenêtre thermique dans les études à plusieurs niveaux trophiques. Dans le contexte des changements climatiques, cela est d'autant plus important que les organismes seront certainement plus souvent exposés à des températures proches des limites de leur fenêtre thermique. Par conséquent, de faibles variations de température pourront avoir des effets importants sur ces organismes.

De nombreux modèles ont été développés afin de prédire comment la prédation intraguilde et la productivité du milieu influencent la persistance et la stabilité des communautés intraguildes (Borer *et al.* 2003; Borer *et al.* 2007; Briggs & Borer 2005; Diehl & Feissel 2000; Hall 2011; Holt & Polis 1997). Ces modèles utilisent différents types de réponses fonctionnelles, principalement les modèles de type I (réponse fonctionnelle linéaire) et de type II (réponse fonctionnelle saturant à haute densité de proies) mais, à ce jour, aucune expérience empirique n'a testé ces deux types de modèles et déterminé celui qui représente le mieux la réponse fonctionnelle d'un prédateur intraguilde. Nous avons donc comparé les prédictions de ces deux modèles en modifiant les densités de proies dans le système biologique à l'étude. Les prédictions du modèle de type II correspondaient bien aux observations empiriques tandis que celles du modèle de type I surestimaient largement le nombre de proies consommées et l'intensité de la prédation intraguilde. Contrairement à la réponse fonctionnelle de type I, celle de type II limite le nombre de proies consommées par le prédateur intraguilde, limitant ainsi la quantité d'énergie dont il dispose pour se développer et se reproduire (Abrams & Fung 2010; McCann & Hastings 1997; McCann *et al.* 1998). Par conséquent, ce modèle limite les fluctuations importantes des effectifs et favorise davantage la coexistence et la persistance des communautés intraguildes (McCann *et al.* 1998). Ceci contribue à expliquer pourquoi, en nature, les communautés intraguildes sont plus stables et persistantes que ce qui est prédit par les modèles utilisant une réponse fonctionnelle de type I (Borer *et al.* 2007; Holt & Polis 1997; Holt & Huxel 2007). Etant donné l'implication majeure du type de réponse fonctionnelle sur la dynamique des populations, il serait intéressant de multiplier les expériences avec d'autres systèmes biologiques afin de généraliser les résultats de notre étude. Comme la plupart des prédateurs démontrent une réponse fonctionnelle de type II (Jeschke *et al.* 2002), on peut s'attendre à ce qu'il en soit de même pour les prédateurs intraguildes.

Par la suite, nous avons dérivé le modèle de réponse fonctionnelle de type II pour prédateur intraguilde afin d'y inclure l'effet de la température. En accord avec les prédictions du modèle, nos résultats expérimentaux démontrent que le nombre de proies consommées par le prédateur intraguilde ainsi que la fréquence des interactions intraguildes augmentent lorsque la température s'accroît. L'analyse de modèle a ensuite révélé que ce résultat est dû à l'effet de la température sur le comportement du prédateur intraguilde : lorsque la température s'accroît, le prédateur intraguilde (*C. maculata*) est plus efficace pour trouver et manipuler ses proies, augmentant ainsi le nombre de proies consommées et la probabilité de rencontrer une proie intraguilde. Selon nos résultats, on peut s'attendre à ce que la fréquence des interactions intraguildes augmente avec les changements climatiques, ce qui pourrait avoir des conséquences importantes pour la dynamique et la structure des communautés. Néanmoins, comme le montrent nos résultats, lorsque la densité de proies extraguildes augmente, la prédation intraguilde est moins fréquente. Puisque la température et la densité de proies devraient augmenter avec les changements climatiques, il est donc difficile de prédire la fréquence des interactions intraguildes. Une approche complémentaire serait d'intégrer notre modèle de réponse fonctionnelle dans un modèle populationnel afin de déterminer l'effet de la température sur la stabilité et la persistance des communautés intraguildes.

Dans un dernier temps, nous avons soumis le système biologique étudié à des pics de chaleur (30 ou 40°C) quotidiens ou deux fois par semaine. Selon les prédictions des modèles développés dans les chapitres 4 et 6, les températures élevées diminuent le nombre de proies consommées par les prédateurs ainsi que l'efficacité énergétique (estimée pour le gain de poids) de ces derniers et la fréquence des interactions intraguildes. Dans cette expérience, nous avons trouvé que l'impact des coccinelles sur les populations de pucerons était diminué par les températures extrêmes et que le poids des larves de coccinelle était moins élevé dans les traitements les plus sévères en termes d'amplitude et de fréquence. Ces résultats semblent coïncider avec les prédictions des modèles mais une mesure directe du nombre de proies consommées serait nécessaire pour s’en assurer. Dans le même ordre d’idée, on pourrait s’attendre à ce que les températures extrêmes diminuent la fréquence des interactions intraguildes et donc favorisent la coexistence des espèces (au moins à court terme). Il serait donc intéressant de réaliser une expérience similaire à la nôtre avec des prédateurs intraguildes et leurs proies.

Globalement, les températures extrêmes n’ont eu aucun effet sur les plantes, peu d’effets sur les larves de coccinelle et des effets majeurs sur la fécondité et l’abondance des pucerons. La sensibilité relative de chaque niveau trophique suggère que les températures extrêmes risquent, à plus long terme, d’altérer les interactions trophiques, perturbant ainsi le fonctionnement actuel des écosystèmes. Néanmoins, nos résultats démontrent que la chaîne trophique étudiée était plus résistante aux températures extrêmes en présence de coccinelles qu’en leur absence : l'abondance de pucerons n'a pas été influencée par les températures extrêmes en présence de *C. maculata*. Cette observation illustre deux points : (1) il est essentiel de tenir compte des interactions trophiques car ces dernières peuvent modifier considérablement l’impact des changements climatiques, (2) les écosystèmes incluant des prédateurs qui régulent fortement les populations d’herbivores seront certainement plus résistants aux changements climatiques que ceux sans prédateurs, lesquels sont davantage influencés par les facteurs abiotiques. Ces résultats concordent avec ceux de Bannerman *et al.* (2011) et Wilmers & Post (2006) et suggèrent que, pour conserver l’intégrité des écosystèmes actuels, il est important de protéger les grands prédateurs qui régulent les populations de proies et diminuent ainsi les effets des facteurs abiotiques sur ces dernières.

Pour conclure, grâce à la combinaison de modèles théoriques et d’études empiriques, notre étude améliore la compréhension des effets de la température et de ses variations sur les pucerons et leurs ennemis naturels. Nos résultats démontrent que la température modifie profondément le comportement des larves de coccinelles, ce qui se répercute sur leur réponse fonctionnelle, leur efficacité énergétique et la fréquence des interactions prédateur-proie. Mais plus intéressant encore, nous sommes les premiers à démontrer qu’un accroissement de la température augmente la fréquence des interactions intraguildes chez deux prédateurs de pucerons. Cette découverte illustre l’importance de considérer la température dans l’étude des systèmes multitrophiques qui sont caractéristiques des écosystèmes naturels (Arim & Marquet 2004; Tylianakis *et al.* 2008; Van der Putten *et al.* 2010). Néanmoins, comme le montrent nos résultats, les effets de la température sur les systèmes multitrophiques sont très complexes car ils affectent à la fois les organismes et les interactions qu'ils entretiennent. De plus, chaque organisme (Dixon *et al.* 2009) ou interaction trophique a sa propre sensibilité thermique, ce qui rend difficile toute généralisation. Et enfin, l'effet de la température dépend aussi de sa variabilité, ce qui, jusqu'à présent, est peu souvent pris en compte dans les études. L'utilisation de modèles est une façon efficiente d'aborder cette problématique multifacette car ces derniers permettent de mieux comprendre les mécanismes sous-jacents et, éventuellement, de généraliser les résultats obtenus. Néanmoins, il sera important de multiplier les études afin de paramétrer ces modèles, de les tester avec des systèmes biologiques variés afin de trouver des patrons généraux qui permettent de mieux comprendre les effets des changements climatiques sur les communautés naturelles.

2. Perspectives de recherche

Dans la présente étude, nous avons combiné la modélisation aux expériences empiriques, ce qui, selon nous, devrait être une approche plus fréquemment adoptée en écologie. Trop souvent, les modèles s'écartent de la réalité du terrain faute d'observations et/ou de paramètres adéquats. D'un autre côté, la conception et la réalisation d'expériences prenant en compte la complexité des systèmes biologiques constituent des tâches ardues. De plus, leurs résultats peuvent rarement être généralisés car les mécanismes sous-jacents ne sont pas étudiés et/ou compris. Lorsque les résultats expérimentaux s'appuient sur un modèle théorique et permettent de valider ce dernier, alors on peut considérer que le modèle reflète bien la réalité biologique et que les mécanismes expliquant les résultats sont bien compris. D'un autre côté, lorsque les prédictions théoriques et les résultats expérimentaux ne concordent pas, la recherche doit se poursuivre pour trouver une explication, ce qui, selon nous, est positif et constructif.

Ainsi, nous avons trouvé que le paramètre « *handling time* » de l'équation du disque (Holling 1959) surestime largement la valeur observée du temps de manipulation et que cette différence dépend de la température (résultat non présenté dans la thèse). Selon

Jeschke *et al.* (2002), le « *handling time* » ne dépend pas seulement du temps de manipulation mais aussi du temps de digestion, ce qui expliquerait ce résultat. Puisque le temps de digestion et le temps de manipulation varient selon l'espèce de prédateur considérée (Jeschke *et al.* 2002) et n'ont probablement pas la même réponse à la température (Dell *et al.* 2011), alors il semble inapproprié de combiner ces deux processus en un seul paramètre. De plus, le « *handling time* » est utilisé dans de nombreux modèles populationnels et contribue à la stabilité et à la connectivité des réseaux trophiques en limitant le taux de prédation et donc les fluctuations importantes des effectifs (McCann *et al.* 1998; Petchey *et al.* 2010; Rall *et al.* 2010). Dans le futur, il sera alors important de mieux comprendre quels sont les différents processus liés à ce paramètre et de déterminer l'influence de la température sur ces derniers.

Comme nous avons pu le voir dans cette étude, la température a un effet important sur la fréquence des interactions intraguildes. Selon nos résultats, à faible température la proie intraguilde bénéficie d'un refuge temporel dans lequel la prédation intraguilde est moins fréquente. De tels refuges pourraient en partie expliquer pourquoi les communautés intraguildes sont plus stables et persistantes que ne le prédisent les modèles (Amarasekare 2007; 2008). Il serait donc intéressant de déterminer l'occurrence de ces refuges et leurs effets sur les interactions intraguildes en milieu naturel. La détection de la prédation intraguilde en milieu naturel est désormais possible grâce aux techniques de biologie moléculaire qui permettent d'analyser le contenu gastrique des prédateurs à partir de l'acide désoxyribonucléique de leurs proies (Gagnon *et al.* 2011). Une expérience pertinente consisterait donc à mesurer l'intensité de la prédation intraguilde au cours de la saison estivale. Selon nos résultats, on peut émettre l'hypothèse que la prédation intraguilde sera moins fréquente en début et fin de saison lorsque les températures sont plus froides qu'en plein été. Néanmoins, il faudra aussi tenir compte des densités de prédateurs intraguildes et de proies extra- et intraguildes qui fluctuent dans le temps et influencent aussi la fréquence des interactions intraguildes.

Plusieurs études ont démontré que les quantités de composés chimiques émises par les plantes augmentent lorsque la température s'accroît (Penuelas 2008; Whittaker 2001). En revanche, les effets de la température sur l'émission et la réception des signaux chimiques chez les insectes sont très peu connus. Pourtant, la signalisation chimique représente le principale mode de communication pour ces derniers. Par exemple, lorsque des larves de coccinelles exploitent une colonie de pucerons, elles déposent des traces larvaires qui inhibent la ponte des coccinelles adultes (Fréchette *et al.* 2003; Hemptinne *et al.* 2001). Ce comportement d'inhibition contribue à réduire le cannibalisme ou la prédation intraguilde des œufs par les prédateurs déjà présents dans la colonie (Doumbia *et al.* 1998; Meisner *et al.* 2011). Comme nous avons pu le voir, la température joue un rôle important sur la fréquence des interactions intraguildes mais son influence sur l'émission des traces larvaires et la réception de ce signal par les adultes n'est pas connue. Si la réponse des femelles aux traces larvaires est plus marquée à haute température alors, contrairement aux résultats que nous avons observés, la fréquence des interactions intraguildes devrait diminuer en raison de l'inhibition du comportement de ponte. Dans le futur, il sera donc pertinent de s'intéresser aux effets de la température sur l'écologie chimique des insectes, ce qui pourrait conduire à des découvertes inattendues.

Sources documentaires

Abrams, P.A. & Fung, S.R. (2010) Prey persistence and abundance in systems with intraguild predation and type-2 functional responses. *Journal of Theoretical Biology* 264: 1033-1042

Agriculture et Agroalimentaire Canada (2006) Profil de la culture du poivron de serre au Canada, programme de réduction des risques liés aux pesticides. Centre pour la lutte antiparasitaire, Ottawa

Amarasekare, P. (2000) Coexistence of competing parasitoids on a patchily distributed host: local vs. spatial mechanisms. *Ecology* 81: 1286-1296

Amarasekare, P. (2007) Trade-offs, temporal variation, and species coexistence in communities with intraguild predation. *Ecology* 88: 2720-2728

Amarasekare, P. (2008) Coexistence of intraguild predators and prey in resource-rich environments. *Ecology* 89: 2786-2797

Arim, M. & Marquet, P.A. (2004) Intraguild predation: a widespread interaction related to species biology. *Ecology Letters* 7: 557-564

Asin, L. & Pons, X. (2001) Effect of high temperature on the growth and reproduction of corn aphids (Homoptera: Aphididae) and implications for their population dynamics on the Northeastern Iberian peninsula. *Environmental Entomology* 30: 1127-1134

Ayres, M.P. & Lombardero, M.J. (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment* 262: 263-286

Bale, J.S. (2002) Insects and low temperatures: from molecular biology to distributions and abundance. *Philosophical Transactions of the Royal Society B: Biological Sciences* 357: 849-862

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C. & Farrar, J. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8: 1-16

Bannerman, J.A., Gillespie, D.R. & Roitberg, B.D. (2011) The impacts of extreme and fluctuating temperatures on trait mediated indirect aphid–parasitoid interactions. *Ecological Entomology* 36: 490-498

Barbosa, P., Saunders, J.A. & Waldvogel, M. (1982) Plant-mediated variation in herbivore suitability and parasitoid fitness. Proceedings of the 5th International Symposium in Insect-Plant Relationships, Wageningen

Barton, B.T., Beckerman, A.P. & Schmitz, O.J. (2009) Climate warming strengthens indirect interactions in an old-field food web. *Ecology* 90: 2346-2351

Barton, B.T. (2011) Local adaptation to temperature conserves top-down control in a grassland food web. *Proceedings of the Royal Society B: Biological Sciences* 278: 3102-3107

Bascompte, J., Jordano, P. & Olesen, J.M. (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312: 431-433

Bayhan, E., Ölmez-Bayhan, S., Ulusoy, M.R. & Brown, J.K. (2005) Effect of temperature on the biology of *Aphis punicae* (Passerini) (Homoptera: Aphididae) on pomegranate. *Environmental Entomology* 34: 22-26

Beckerman, A.P., Petchey, O.L. & Warren, P.H. (2006) Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences* 103: 13745-13749

Bensadia, F., Boudreault, S., Guay, J.F., Michaud, D. & Cloutier, C. (2006) Aphid clonal resistance to a parasitoid fails under heat stress. *Journal of Insect Physiology* 52: 146-157

Benton, A.H. & Crump, A.J. (1981) Observations on the spring and summer behavior of the 12-spotted ladybird beetle, *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae). *Journal of the New York Entomological Society* 89: 102-108

Blackman, R.L. & Eastop, V.F. (2000) Aphids on the World's crops. An identification and information guide. John Wiley & Sons, New York

Boiteau, G. (1983) The arthropod community of potato fields in New Brunswick, 1979-1981. *The Canadian Entomologist* 115: 847-853

Bolker, B.M. (2008) Ecological models and data in R. Princeton University Press, Princeton

Borer, E.T., Briggs, C.J., Murdoch, W.W. & Swarbrick, S.L. (2003) Testing intraguild predation theory in a field system: does numerical dominance shift along a gradient of productivity? *Ecology Letters* 6: 929-935

Borer, E.T. (2006) Does adding biological detail increase coexistence in an intraguild predation model? *Ecological Modelling* 196: 447-461

Borer, E.T., Briggs, C.J. & Holt, R.D. (2007) Predators, parasitoids, and pathogens: a cross-cutting examination of intraguild predation theory. *Ecology* 88: 2681-2688

Bouchard, D. & Tourneur, J.C. (1981) Bio-écologie d'*Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) prédateur du puceron du pommier, *Aphis pomi* DeGeer (Homoptera: Aphididae). *Annales de la Société Entomologique du Québec* 26: 119-130

Bourchier, R.S. & Smith, S.M. (1996) Influence of environmental conditions and parasitoid quality on field performance of *Trichogramma minutum*. *Entomologia Experimentalis et Applicata* 80: 461-468

Briere, J., Pracros, P., Le Roux, A. & Pierre, J. (1999) A novel rate model of temperature-dependent development for arthropods. *Environmental Entomology* 28: 22-29

Briggs, C.J. & Borer, E.T. (2005) Why short-term experiments may not allow long-term predictions about intraguild predation. *Ecological Applications* 15: 1111-1117

Brodeur, J. & Rosenheim, J.A. (2000) Intraguild interactions in aphid parasitoids. *Entomologia Experimentalis et Applicata* 97: 93-108

Brodeur, J., Cloutier, C. & Gillespie, D. (2002) Higher-order predators in greenhouse systems. *IOBC WPRS Bulletin* 25: 33-36

Brose, U., Williams, R.J. & Martinez, N.D. (2006) Allometric scaling enhances stability in complex food webs. *Ecology Letters* 9: 1228-1236

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology* 85: 1771-1789

Brown, M.W. (2004) Role of aphid predator guild in controlling spirea aphid populations on apple in West Virginia, USA. *Biological Control* 29: 189-198

Butchart, S.H.M., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C. & Bruno, J. (2010) Global biodiversity: indicators of recent declines. *Science* 328: 1164-1168

Cammell, M.E. & Knight, J.D. (1992) Effects of climatic change on the population dynamics of crop pests. *Advances in Ecological Research* 22: 117-162

Cannon, R.J.C. (1998) The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology* 4: 785-796

Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002) Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415: 426-429

Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M. & Jouseau, C. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443: 989-992

Carter, M.C., Sutherland, D. & Dixon, A.F.G. (1984) Plant structure and the searching efficiency of coccinellid larvae. *Oecologia* 63: 394-397

Cave, R.D. & Gaylor, M.J. (1989) Functional response of *Telenomus reynoldsi* [Hym.: Scelionidae] at five constant temperatures and in an artificial plant arena. *BioControl* 34: 3-10

Chacón, J.M. & Heimpel, G.E. (2010) Density-dependent intraguild predation of an aphid parasitoid. *Oecologia* 164: 213-220

Chen, F., Ge, F. & Parajulee, M.N. (2005) Impact of elevated CO_2 on tri-trophic interaction of *Gossypium hirsutum*, *Aphis gossypii*, and *Leis axyridis*. *Environmental Entomology* 34: 37-46

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C. & Carrara, A. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437: 529-533

Cocuzza, G.E., De Clercq, P., Lizzio, S., Van de Veire, M., Tirry, L., Degheele, D. & Vacante, V. (1997) Life tables and predation activity of *Orius laevigatus* and *O. albidipennis* at three constant temperatures. *Entomologia Experimentalis et Applicata* 85: 189-198

Coderre, D. & Tourneur, J.C. (1988) Déclin estival des populations aphidiennes du maïs. *Revue d'Entomologie du Québec* 32: 16-24

Colton, T.F. (1987) Extending functional response models to include a second prey type: an experimental test. *Ecology* 68: 900-912

Corless, R.M., Gonnet, G.H., Hare, D.E.G., Jeffrey, D.J. & Knuth, D.E. (1996) On the Lambert W function. *Advances in Computational Mathematics* 5: 329-359

Coviella, C.E. & Trumble, J.T. (1999) Effects of elevated atmospheric carbon dioxide on insect–plant interactions. *Conservation Biology* 13: 700-712

Davis, J.A., Radcliffe, E.B. & Ragsdale, D.W. (2006) Effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera: Aphididae). *Environmental Entomology* 35: 1461-1468

Davison, R., Jacquemyn, H., Adriaens, D., Honnay, O., De Kroon, H. & Tuljapurkar, S. (2010) Demographic effects of extreme weather events on a short lived calcareous grassland species: stochastic life table response experiments. *Journal of Ecology* 98: 255-267

De Boeck, H.J., Dreesen, F.E., Janssens, I.A. & Nijs, I. (2010) Climatic characteristics of heat waves and their simulation in plant experiments. *Global Change Biology* 16: 1992-2000

Dell, A.I., Pawar, S. & Savage, V.M. (2011) Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences* 108: 10591-10596

Diehl, S. & Feissel, M. (2000) Effects of enrichment on three-level food chains with omnivory. *American Naturalist* 155: 200-218

Diehl, S. & Feissel, M. (2001) Intraguild prey suffer from enrichment of their resources: a microcosm experiment with ciliates. *Ecology* 82: 2977-2983

Dixon, A.F.G. (1977) Aphid ecology: life cycles, polymorphism, and population regulation. *Annual Review of Ecology and Systematics* 8: 329-353

Dixon, A.F.G. (1985) Structure of aphid populations. *Annual Review of Entomology* 30: 155-174

Dixon, A.F.G. (1998) Aphid ecology. Chapman and Hall, New York

Dixon, A.F.G., Jarošik, V. & Honěk, A. (2005) Thermal requirements for development and resource partitioning in aphidophagous guilds. *European Journal of Entomology* 102: 407-411

Dixon, A.F.G., Honěk, A., Keil, P., Kotela, M.A.A., Šizling, A.L. & Jarošík, V. (2009) Relationship between the minimum and maximum temperature thresholds for development in insects. *Functional Ecology* 23: 257-264

Doumbia, M., Hemptinne, J.L. & Dixon, A.F.G. (1998) Assessment of patch quality by ladybirds: role of larval tracks. *Oecologia* 113: 197-202

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate extremes: observations, modeling, and impacts. *Science* 289: 2068-2074

Eggleston, D.B. (1990) Behavioural mechanisms underlying variable functional responses of blue crabs, *Callinectes sapidus* feeding on juvenile oysters, *Crassostrea virginica*. *Journal of Animal Ecology* 59: 615-630

Elliott, N.C., Kieckhefer, R.W. & Beck, D.A. (2000) Adult coccinellid activity and predation on aphids in spring cereals. *Biological Control* 17: 218-226

Emden, H.F.V., Eastop, V.F., Hughes, R.D. & Way, M.J. (1969) The ecology of *Myzus persicae*. *Annual Review of Entomology* 14: 197-270

Englund, G., Ohlund, G., Hein, C.L. & Diehl, S. (2011) Temperature dependence of the functional response. *Ecology Letters* 14: 914-921

Environment Canada (2010) National climate data and information archive. www.climate.weatheroffice.gc.ca, Consulté en février 2010

Ferran, A. & Larroque, M.M. (1979) Influence des facteurs abiotiques sur la physiologie alimentaire des larves de la coccinelle aphidiphage, *Semiadalia undecimnotata* [Col.: Coccinellidae]; I. Action de la température. *BioControl* 24: 403-410

Finke, D.L. & Denno, R.F. (2002) Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* 83: 643-652

Finke, D.L. & Denno, R.F. (2006) Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia* 149: 265-275

Finke, D.L. & Snyder, W.E. (2010) Conserving the benefits of predator biodiversity. *Biological Conservation* 143: 2260-2269

Firlej, A., Chouinard, G. & Coderre, D. (2006) A meridic diet for the rearing of *Hyaliodes vitripennis* (Hemiptera: Miridae), a predator of mites in apple orchards. *Biocontrol Science and Technology* 16: 743-751

Flinn, P.W. (1991) Temperature-dependent functional response of the parasitoid *Cephalonomia waterstoni* (Gahan) (Hymenoptera: Bethylidae) attacking rusty grain beetle larvae (Coleoptera: Cucujidae). *Environmental Entomology* 20: 872-876

Francis, F., Haubruge, E. & Gaspar, C. (2000) Influence of host plants on specialist/generalist aphids and on the development of *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology* 97: 481-486

Francis, F., Haubruge, E., Hastir, P. & Gaspar, C. (2001) Effect of aphid host plant on development and reproduction of the third trophic tevel, the predator *Adalia bipunctata* (Coleoptera: Coccinellidae). *Environmental Entomology* 30: 947-952

Francke, D.L., Harmon, J.P., Harvey, C.T. & Ives, A.R. (2008) Pea aphid dropping behavior diminishes foraging efficiency of a predatory ladybeetle. *Entomologia Experimentalis et Applicata* 127: 118-124

Fréchette, B., Alauzet, C. & Hemptinne, J.L. (2003) Oviposition behaviour of the two-spot ladybird beetle *Adalia bipunctata* (L.)(Coleoptera: Coccinellidae) on plants with conspecific larval tracks. *Arquipélago–Life and Marine Science, Supplement* 5: 73–77

Gagnon, A.È., Heimpel, G.E. & Brodeur, J. (2011) The ubiquity of intraguild predation among predatory arthropods. *PLoS ONE*: in press

Gardiner, M.M. & Landis, D.A. (2007) Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Hemiptera: Aphididae) biological control in cage studies. *Biological Control* 40: 386-395

Gillespie, D.R., Nasreen, A., Moffat, C.E., Clarke, P. & Roitberg, B.D. (2012) Effects of simulated heat waves on an experimental community of pepper plants, green peach aphids, and two parasitoid species. *Oikos* 121: 149-159

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001) Effects of size and temperature on metabolic rate. *Science* 293: 2248-2251

Giroux, S., Duchesne, R.M. & Coderre, D. (1995) Predation of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) by *Coleomegilla maculata* (Coleoptera: Coccinellidae): comparative effectiveness of predator developmental stages and effect of temperature. *Environmental Entomology* 24: 748-754

Gordon, R.D. (1985) The coccinellidae (Coleoptera) of America north of Mexico. *Journal of the New York Entomological Society* 96: 1-912

Grasswitz, T.R. & Burts, E.C. (1995) Effect of native natural enemies and augmentative releases of *Chrysoperla rufilabris* Burmeister and *Aphidoletes aphidimyza* (Rondani) on the population dynamics of the green apple aphid, *Aphis pomi* De Geer. *International Journal of Pest Management* 41: 176-183

Greenblatt, J.A., Barbosa, P. & Montgomery, M.E. (1982) Host's diet effects on nitrogen utilization efficiency for two parasitoid species: *Brachymeria intermedia* and *Coccygomimus turionellae*. *Physiological Entomology* 7: 263-267

Gresens, S.E., Cothran, M.L. & Thorp, J.H. (1982) The influence of temperature on the functional response of the dragonfly *Celithemis fasciata* (Odonata: Libellulidae). *Oecologia* 53: 281-284

Gutierrez, A.P., Daane, K.M., Ponti, L., Walton, V.M. & Ellis, C.K. (2008) Prospective evaluation of the biological control of vine mealybug: refuge effects and climate. *Journal of Applied Ecology* 45: 524-536

Hall, R.J. (2011) Intraguild predation in the presence of a shared natural enemy. *Ecology* 92: 352-361

Harmon, J.P., Moran, N.A. & Ives, A.R. (2009) Species response to environmental change: impacts of food web interactions and evolution. *Science* 323: 1347-1350

Harrington, R., Woiwod, I. & Sparks, T. (1999) Climate change and trophic interactions. *Trends in Ecology & Evolution* 14: 146-150

Harrington, R., Fleming, R.A. & Woiwod, I.P. (2001) Climate change impacts on insect management and conservation in temperate regions: can they be predicted? *Agricultural and Forest Entomology* 3: 233-240

Havelka, J. (1980) Effect of temperature on the developmental rate of preimaginal stages of *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). *Entomologia Experimentalis et Applicata* 27: 83-90

Havelka, J. & Zemek, R. (1999) Life table parameters and oviposition dynamics of various populations of the predacious gall-midge *Aphidoletes aphidimyza*. *Entomologia Experimentalis et Applicata* 91: 481-484

Hazell, S.P., Neve, B.P., Groutides, C., Douglas, A.E., Blackburn, T.M. & Bale, J.S. (2010) Hyperthermic aphids: insights into behaviour and mortality. *Journal of Insect Physiology* 56: 123-131

Hemptinne, J.L., Lognay, G., Doumbia, M. & Dixon, A.F.G. (2001) Chemical nature and persistence of the oviposition deterring pheromone in the tracks of the larvae of the two spot ladybird, *Adalia bipunctata* (Coleoptera: Coccinellidae). *Chemoecology* 11: 43-47

Hindayana, D., Meyhöfer, R., Scholz, D. & Poehling, H.M. (2001) Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators. *Biological Control* 20: 236-246

Hodek, I. & Honěk, A. (1996) Ecology of Coccinellidae. Kluwer, Boston

Hoekman, D. (2010) Turning up the heat: temperature influences the relative importance of top-down and bottom-up effects in pitcher plant inquiline communities. *Ecology* 91: 2819-2825

Holling, C.S. (1959) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* 91: 385-398

Holopainen, J.K. & Kainulainen, P. (2004) Reproductive capacity of the grey pine aphid and allocation response of Scots pine seedlings across temperature gradients: a test of hypotheses predicting outcomes of global warming. *Canadian Journal of Forest Research* 34: 94-102

Holt, R.D. & Polis, G.A. (1997) A theoretical framework for intraguild predation. *American Naturalist* 149: 745-764

Holt, R.D. & Huxel, G.R. (2007) Alternative prey and the dynamics of intraguild predation: theoretical perspectives. *Ecology* 88: 2706-2712

Honěk, A. (1985) Activity and predation of *Coccinella septempunctata* adults in the field (Col., Coccinellidae). *Zeitschrift für Angewandte Entomologie* 100: 399-409

Honěk, A. & Kocourek, F. (1988) Thermal requirements for development of aphidophagous Coccinellidae (Coleoptera), Chrysopidae, Hemerobiidae (Neuroptera), and Syrphidae (Diptera): some general trends. *Oecologia* 76: 455-460

Hunt-Joshi, T.R., Root, R.B. & Blossey, B. (2005) Disruption of weed biological control by an opportunistic mirid predator. *Ecological Applications* 15: 861-870

IPCC (2007) Climate Change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Ives, A.R. & Carpenter, S.R. (2007) Stability and diversity of ecosystems. *Science* 317: 58-62

Jalali, M.A., Tirry, L., Arbab, A. & De Clercq, P. (2010a) Temperature-dependent development of the two-spotted ladybeetle, *Adalia bipunctata*, on the green peach aphid, *Myzus persicae*, and a factitious food under constant temperatures. *Journal of Insect Science* 10: 1536-1552

Jalali, M.A., Tirry, L. & De Clercq, P. (2010b) Effect of temperature on the functional response of *Adalia bipunctata* to *Myzus persicae*. *BioControl* 55: 261-269

Janssen, A., Sabelis, M.W., Magalhaes, S., Montserrat, M. & van der Hammen, T. (2007) Habitat structure affects intraguild predation. *Ecology* 88: 2713-2719

Jentsch, A., Kreyling, J. & Beierkuhnlein, C. (2007) A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment* 5: 365-374

Jeoung, Y.S., Choe, Y.S., Oh, I.S., Han, K.H., Seo, M.J. & Youn, Y.N. (2003) Biological characteristics of the aphid-eating gall-midge, *Aphidoletes* *aphidimyza* (Diptera : Cecidomyiidae) as a biological control agents of aphids. *Korean Journal of Applied Entomology* 42: 241-248

Jeschke, J.M., Kopp, M. & Tollrian, R. (2002) Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs* 72: 95-112

Jones, T.H., Thompson, L.J., Lawton, J.H., Bezemer, T.M., Bardgett, R.D., Blackburn, T.M., Bruce, K.D., Cannon, P.F., Hall, G.S. & Hartley, S.E. (1998) Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. *Science* 280: 441-443

Juliano, S.A. (2001) Nonlinear curve fitting: predation and functional response curve. In: Scheiner S.M., Gurevitch J. (eds) Design and analysis of ecological experiments. Chapman and Hall, New York, pp 178-196

Kagata, H., Nakamura, M. & Ohgushi, T. (2005) Bottom-up cascade in a tri-trophic system: different impacts of host-plant regeneration on performance of a willow leaf beetle and its natural enemy. *Ecological Entomology* 30: 58-62

Kennedy, J.S., Day, M.F. & Eastop, V.F. (1962) A conspectus of aphids as vectors of plant viruses. Commonwealth Institute of Entomology, London

Kivan, V. (2000) Optimal intraguild foraging and population stability. *Theoretical Population Biology* 58: 79-94

Kondoh, M. (2003) Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299: 1388-1391

Lamb, R. & Gerber, G. (1985) Effects of temperature on the development, growth, and survival of larvae and pupae of a north-temperate chrysomelid beetle. *Oecologia* 67: 8-18

Lawler, S.P. & Morin, P.J. (1993) Food web architecture and population dynamics in laboratory microcosms of protists. *American Naturalist* 141: 675-686

Losey, J.E. & Denno, R.F. (1998) The escape response of pea aphids to foliar-foraging predators: factors affecting dropping behaviour. *Ecological Entomology* 23: 53-61

Lucas, E., Coderre, D. & Brodeur, J. (1998) Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology* 73: 1084-1092

Lucas, E. & Brodeur, J. (1999) Oviposition site selection by the predatory midge *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). *Environmental Entomology* 28: 622-627

Lucas, E. & Brodeur, J. (2001) A fox in sheep's clothing: furtive predator benefit from the communal defense of their prey. *Ecology* 82: 3246-3250

Lucas, E. (2005) Intraguild predation among aphidophagous predators. *European Journal of Entomology* 102: 351-364

Lucas, E. & Rosenheim, J.A. (2011) Influence of extraguild prey density on intraguild predation by heteropteran predators: a review of the evidence and a case study. *Biological Control* 59: 61-67

Mack, T.P., Bajusz, B.A., Nolan, E.S. & Smilowitz, Z. (1981) Development of a temperature-mediated functional response equation. *Environmental Entomology* 10: 573-579

Mack, T.P. & Smilowitz, Z. (1982) Using temperature-mediated functional response models to predict the impact of *Coleomegilla maculata* (DeGeer) adults and 3rd-instar larvae on green peach aphids. *Environmental Entomology* 11: 46-52

Malais, M. & Ravensberg, W.J. (1993) Connaître et reconnaître : mode de vie des ravageurs de serre et de leurs ennemis naturels. Koppert B.V., Berkel en Rodenrijs

Markkula, M., Tiittanen, K., Hussey, N.W. & Scopes, N. (1985) Biology of the midge *Aphidoletes aphidimyza* and its potential for biological control. In: Hussey N.W., Scopes N. (eds) Biological pest control: the glasshouse experience. Cornell University Press, Ithaca, New York, pp 74-81

Mayntz, D. (2001) Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. *Oecologia* 127: 207-213

McCann, K.S. & Hastings, A. (1997) Re-evaluating the omnivory–stability relationship in food webs. *Proceedings of the Royal Society B: Biological Sciences* 264: 1249-1254

McCann, K.S., Hastings, A. & Huxel, G.R. (1998) Weak trophic interactions and the balance of nature. *Nature* 395: 794-798

McCann, K.S. (2000) The diversity–stability debate. *Nature* 405: 228-233

Meisner, M.H., Harmon, J.P. & Ives, A.R. (2011) Response of coccinellid larvae to conspecific and heterospecific larval tracks: a mechanism that reduces cannibalism and intraguild predation. *Environmental Entomology* 40: 103-110

Menon, A., Flinn, P.W. & Dover, B.A. (2002) Influence of temperature on the functional response of *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae), a parasitoid of *Rhyzopertha dominica* (Coleoptera: Bostrichidae). *Journal of Stored Products Research* 38: 463-469

Messenger, P.S. (1968) Bioclimatic studies of the aphid parasite *Praon exsoletum*. I. Effects of temperature on the functional response of females to varying host densities. *The Canadian Entomologist* 100: 728-741

Messina, F.J. & Hanks, J.B. (1998) Host plant alters the shape of the functional response of an aphid predator (Coleoptera: Coccinellidae). *Environmental Entomology* 27: 1196-1202

Mironidis, G.K. & Savopoulou-Soultani, M. (2008) Development, survivorship, and reproduction of *Helicoverpa armigera* (Lepidoptera: Noctuidae) under constant and alternating temperatures. *Environmental Entomology* 37: 16-28

Mittler, R. (2006) Abiotic stress, the field environment and stress combination. *Trends in Plant Science* 11: 15-19

Morgan, D., Walters, K.F.A. & Aegerter, J.N. (2007) Effect of temperature and cultivar on pea aphid, *Acyrthosiphon pisum* (Hemiptera: Aphididae) life history. *Bulletin of Entomological Research* 91: 47-52

Morin, P. (1999) Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology* 80: 752-760

Müller, C.B. & Brodeur, J. (2002) Intraguild predation in biological control and conservation biology. *Biological Control* 25: 216-223

Mylius, S.D., Klumpers, K., de Roos, A.M. & Persson, L. (2001) Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *American Naturalist* 158: 259-276

Newman, J.A. (2006) Using the output from global circulation models to predict changes in the distribution and abundance of cereal aphids in Canada: a mechanistic modeling approach. *Global Change Biology* 12: 1634-1642

Nijveldt, W. (1988) Cecidomyiidae. Elsevier Science Publishers, New York

Northfield, T.D., Snyder, G.B., Ives, A.R. & Snyder, W.E. (2010) Niche saturation reveals resource partitioning among consumers. *Ecology Letters* 13: 338-348

Obrycki, J.J. & Tauber, M.J. (1978) Thermal requirements for development of *Coleomegilla maculata* (Coleoptera: Coccinellidae) and its parasite *Perilitus* *coccinellae* (Hymenoptera: Braconidae). *The Canadian Entomologist* 110: 407-412

Obrycki, J.J., Ormord, A.M. & Giles, K.L. (1997) Partial life table analysis for larval *Coleomegilla maculata* (Degeer) and *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) in alfalfa. *Journal of the Kansas Entomological Society* 70: 339-346

Olesen, J.E. & Bindi, M. (2002) Consequences of climate change for European agricultural productivity, land use and policy. *European Journal of Agronomy* 16: 239-262

Omkar, A.P. (2004) Temperature-dependent development and immature survival of an aphidophagous ladybeetle, *Propylea dissecta* (Mulsant). *Journal of Applied Entomology* 128: 510-514

Ongagna, P., Giuge, L., Iperti, G. & Ferran, A. (1993) Cycle de développement d'*Harmonia axyridis* (Col. Coccinellidae) dans son aire d'introduction: le Sud-Est de la France. *BioControl* 38: 125-128

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Evolution and Systematics* 37: 637-69

Penuelas, J. (2008) An increasingly scented world. *New Phytologist* 180: 735-738

Persson, L. (1986) Temperature-induced shift in foraging ability in two fish species, roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*): implications for coexistence between poikilotherms. *Journal of Animal Ecology* 55: 829-839

Persson, L., Leonardsson, K., de Roos, A.M., Gyllenberg, M. & Christensen, B. (1998) Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer–resource model. *Theoretical Population Biology* 54: 270-293

Petavy, G., David, J., Gibert, P. & Moreteau, B. (2001) Viability and rate of development at different temperatures in Drosophila: a comparison of constant and alternating thermal regimes. *Journal of Thermal Biology* 26: 29-39

Petchey, O.L., McPhearson, P.T., Casey, T.M. & Morin, P.J. (1999) Environmental warming alters food-web structure and ecosystem function. *Nature* 402: 69-72

Petchey, O.L., Brose, U. & Rall, B.C. (2010) Predicting the effects of temperature on food web connectance. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2081-2091

Peters, R.H. (1986) The ecological implications of body size. Cambridge University Press, Cambridge

Polis, G.A., Myers, C.A. & Holt, R.D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20: 297-330

Porter, J.H., Parry, M.L. & Carter, T.R. (1991) The potential effects of climatic change on agricultural insect pests. *Agricultural and Forest Meteorology* 57: 221-240

Porter, J.R. & Semenov, M.A. (2005) Crop responses to climatic variation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360: 2021–2035

Pörtner, H.O., Bennett, A.F., Bozinovic, F., Clarke, A., Lardies, M.A., Lucassen, M., Pelster, B., Schiemer, F. & Stillman, J.H. (2006) Trade-offs in thermal adaptation: the need for a molecular to ecological integration. *Physiological and Biochemical Zoology* 79: 295-313

Pörtner, H.O. & Farrell, A.P. (2008) Physiology and climate change. *Science* 322: 690-692

Powell, J.R. & Webster, J.M. (2004) Interguild antagonism between biological controls: impact of entomopathogenic nematode application on an aphid predator, *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). *Biological Control* 30: 110-118

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weis, A.E. (1980) Interactions among three trophic jevels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Reviews in Ecology and Systematics* 11: 41-65

R Development Core Team (2011) R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria

Rall, B.C., Guill, C. & Brose, U. (2008) Food web connectance and predator interference dampen the paradox of enrichment. *Oikos* 117: 202-213

Rall, B.C., Vucic-Pestic, O., Ehnes, R.B., Emmerson, M. & Brose, U. (2010) Temperature, predator–prey interaction strength and population stability. *Global Change Biology* 16: 2145-2157

Rochat, J. & Gutierrez, A.P. (2001) Weather-mediated regulation of olive scale by two parasitoids. *Journal of Animal Ecology* 70: 476-490

Rogers, D. (1972) Random search and insect population models. *Journal of Animal Ecology* 41: 369-383

Rosenheim, J.A., H. K. Kaya, Ehler, L.E., J. J. Marois & Jaffee, B.A. (1995) Intraguild predation among biological-control agents: theory and evidence. *Biological Control* 5: 303-335

Rosenheim, J.A. (1998) Higher-order predators and the regulation of insect herbivore populations. *Annual Review of Entomology* 43: 421-447

Rosenheim, J.A. & Corbett, A. (2003) Omnivory and the indeterminacy of predator function: can a knowledge of foraging behavior help? *Ecology* 84: 2538-2548

Rosenheim, J.A. (2007) Intraguild predation: new theoretical and empirical perspectives 1. *Ecology* 88: 2679-2680

Roux, O., Le Lann, C., Van Alphen, J.J.M. & Van Baaren, J. (2010) How does heat shock affect the life history traits of adults and progeny of the aphid parasitoid *Aphidius avenae* (Hymenoptera: Aphidiidae). *Bulletin of Entomological Research* 100: 543-549

Rudolf, V.H.W. (2007) The interaction of cannibalism and omnivory: consequences for community dynamics. *Ecology* 88: 2697-2705

SAS Institute (2008) JMP v.8. SAS Institue, Cary, NC, USA

Savage, V.M., Gillooly, J.F., Woodruff, W.H., West, G.B., Allen, A.P., Enquist, B.J. & Brown, J.H. (2004) The predominance of quarter power scaling in biology. *Functional Ecology* 18: 257-282

Schanderl, H., Ferran, A. & Larroque, M.M. (1985) Les besoins trophiques et thermiques des larves de la coccinelle *Harmonia axyridis* Pallas. *Agronomie* 5: 417-421

Schmitz, O.J., Post, E., Burns, C.E. & Johnston, K.M. (2003) Ecosystem responses to global climate change: moving beyond color mapping. *BioScience* 53: 1199-1205

Schmitz, O.J. (2007) Predator diversity and trophic interactions. *Ecology* 88: 2415-2426

Sih, A., Englund, G. & Wooster, D. (1998) Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution* 13: 350-355

Skalski, G.T. & Gilliam, J.F. (2001) Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology* 82: 3083-3092

Smith, M.D. (2011) The ecological role of climate extremes: current understanding and future prospects. *Journal of Ecology* 99: 651-655

Soares, A.O., Coderre, D. & Schanderl, H. (2003) Effect of temperature and intraspecific allometry on predation by two phenotypes of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Environmental Entomology* 32: 939-944

Stacey, D. (2003) Climate and biological control in organic crops. *International Journal of Pest Management* 49: 205-214

Stadler, B. & Dixon, A.F.G. (2005) Ecology and evolution of aphid–ant interactions. *Annual Review of Ecology and Systematics* 36: 345-372

Steffan, S.A. & Snyder, W.E. (2010) Cascading diversity effects transmitted exclusively by behavioral interactions. *Ecology* 91: 2242-2252

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S. & Lima, M. (2002) Ecological effects of climate fluctuations. *Science* 297: 1292-1296

Stewart, H.C. & Walde, S.J. (1997) The dynamics of *Aphis pomi* De Geer (Homoptera: Aphididae) and its predator, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae), on apple in Nova Scotia. *The Canadian Entomologist* 129: 627-636

Stewart, L.A., Hemptinne, J.L. & Dixon, A.F.G. (1991) Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number, and developmental time. *Functional Ecology* 5: 380-385

Stiling, P., Rossi, A.M., Hungate, B., Dijkstra, P., Hinkle, C.R., Knott Iii, W.M. & Drake, B. (1999) Decreased leaf-miner abundance in elevated CO_2: reduced leaf quality and increased parasitoid attack. *Ecological Applications* 9: 240-244

Straub, C.S., Finke, D.L. & Snyder, W.E. (2008) Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control* 45: 225-237

Thibault, K.M. & Brown, J.H. (2008) Impact of an extreme climatic event on community assembly. *Proceedings of the National Academy of Sciences* 105: 3410–3415

Thompson, D.J. (1978) Towards a realistic predator–prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. *Journal of Animal Ecology* 47: 757-767

Tuda, M., Matsumoto, T., Itioka, T., Ishida, N., Takanashi, M., Ashihara, W., Kohyama, M. & Takagi, M. (2006) Climatic and intertrophic effects detected in 10-year population dynamics of biological control of the arrowhead scale by two parasitoids in southwestern Japan. *Population Ecology* 48: 59-70

Turchin, P. & Kareiva, P. (1989) Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology* 70: 1008-1016

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11: 1351-1363

Uchida, S. & Drossel, B. (2007) Relation between complexity and stability in food webs with adaptive behavior. *Journal of Theoretical Biology* 247: 713-722

Uchida, S., Drossel, B. & Brose, U. (2007) The structure of food webs with adaptive behaviour. *Ecological Modelling* 206: 263-276

Van der Putten, W.H., Macel, M. & Visser, M.E. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2025-2034

Vance-Chalcraft, H.D., Rosenheim, J.A., Vonesh, J.R., Osenberg, C.W. & Sih, A. (2007) The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology* 88: 2689-2696

Vasseur, D.A. & McCann, K.S. (2005) A mechanistic approach for modeling temperature-dependent consumer–resource dynamics. *American Naturalist* 166: 184-198

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science* 277: 494-499

Voigt, W., Perner, J., Davis, A.J., Eggers, T., Schumacher, J., Bährmann, R., Fabian, B., Heinrich, W., Köhler, G. & Lichter, D. (2003) Trophic levels are differentially sensitive to climate. *Ecology* 84: 2444-2453

Voynaud, L. (2008) Prédation intraguilde entre prédateur actif et prédateur furtif au sein d'une guilde aphidiphage. Thèse de maîtrise, Université du Québec à Montréal, Montréal, Canada

Vucic-Pestic, O., Rall, B.C., Kalinkat, G. & Brose, U. (2010) Allometric functional response model: body masses constrain interaction strengths. *Journal of Animal Ecology* 79: 249-256

Vucic-Pestic, O., Ehnes, R.B., Rall, B.C. & Brose, U. (2011) Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Global Change Biology* 17: 1301-1310

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature* 416: 389-395

Walther, G.R. (2010) Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2019-2024

Wang, J.J. & Tsai, J.H. (2007) Development, survival and reproduction of black citrus aphid, *Toxoptera aurantii* (Hemiptera: Aphididae), as a function of temperature. *Bulletin of Entomological Research* 91: 477-487

Warren, L.O. & Tadic, M. (1967) Biological observations on *Coleomegilla maculata* and its role as a predator of the Fall Webworm. *Journal of Economic Entomology* 60: 1492-1495

West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science* 276: 122-126

Whittaker, J.B. (2001) Insects and plants in a changing atmosphere. *Journal of Ecology* 89: 507-518

Williams, R.J. & Martinez, N.D. (2004) Limits to trophic levels and omnivory in complex food webs: theory and data. *American Naturalist* 163: 458-468

Williams, R.J. (2008) Effects of network and dynamical model structure on species persistence in large model food webs. *Theoretical Ecology* 1: 141-151

Wilmers, C.C. & Post, E. (2006) Predicting the influence of wolf provided carrion on scavenger community dynamics under climate change scenarios. *Global Change Biology* 12: 403-409

Xia, J.Y., Van der Werf, W. & Rabbinge, R. (1999) Temperature and prey density on bionomics of *Coccinella septempunctata* (Coleoptera: Coccinellidae) feeding on *Aphis gossypii* (Homoptera: Aphididae) on cotton. *Environmental Entomology* 28: 307-314

Xia, J.Y., Rabbinge, R. & Van der Werf, W. (2003) Multistage functional responses in a ladybeetle–aphid system: scaling up from the laboratory to the field. *Environmental Entomology* 32: 151-162

Yocum, G., Joplin, K. & Denlinger, D. (1991) Expression of heat shock proteins in response to high and low temperature extremes in diapausing pharate larvae of the gypsy moth, *Lymantria dispar*. *Archives of Insect Biochemistry and Physiology* 18: 239-249

Zamani, A.A., Talebi, A.A., Fathipour, Y. & Baniameri, V. (2006) Temperature-dependent functional response of two aphid parasitoids, *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Aphidiidae), on the cotton aphid. *Journal of Pest Science* 79: 183-188

Zamani, A.A., Talebi, A., Fathipour, Y. & Baniameri, V. (2007) Effect of temperature on life history of *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Braconidae), two parasitoids of *Aphis gossypii* and *Myzus persicae* (Homoptera: Aphididae). *Environmental Entomology* 36: 263-271

Zvereva, E.L. & Rank, N.E. (2003) Host plant effects on parasitoid attack on the leaf beetle *Chrysomela lapponica*. *Oecologia* 135: 258-267

Annexe 1

Chapter 5. Calculation details from Eq. 8 to Eq. 9

Starting with the model (Eq. 8) for *C. maculata* exploiting intra- or extraguild prey with a similar search rate ($a_{eg} = a_{ig}$):

$$N_{eg} = N_{0eg} \times (1 - e^{-a_{eg}(t - h_{eg} N_{eg} - h_{ig} N_{ig})}) \tag{A1}$$

$$N_{ig} = N_{0ig} \times (1 - e^{-a_{eg}(t - h_{ig} N_{ig} - h_{eg} N_{eg})}) \tag{A2}$$

We used the Lambert *W* function to solve recursive functions A1 and A2 (see Bolker 2008 for details). This yields:

$$N_{eg} = N_{0eg} - \frac{w(a_{eg} h_{eg} N_{0eg} e^{-a_{eg}(t - h_{eg} N_{0eg} - h_{ig} N_{ig})})}{a_{eg} h_{eg}} \tag{A3}$$

$$N_{ig} = N_{0ig} - \frac{w(a_{eg} h_{ig} N_{0ig} e^{-a_{eg}(t - h_{ig} N_{0ig} - h_{eg} N_{eg})})}{a_{ig} h_{ig}} \tag{A4}$$

Inserting Eq. A4 into Eq. A3 yields:

$$N_{eg} = N_{0eg} - \frac{w(a_{eg} h_{eg} N_{0eg} e^{-a_{eg}(t - h_{eg} N_{0eg} - h_{ig}(N_{0ig} - \frac{w(a_{eg} h_{ig} N_{0ig} e^{-a_{eg}(t - h_{ig} N_{0ig} - h_{eg} N_{eg})})}{a_{ig} h_{ig}}))})}{a_{eg} h_{eg}} \tag{A5}$$

By reversing the Lambert *W* function:

$$-a_{eg} h_{eg}(N_{eg} - N_{0eg}) e^{-a_{eg} h_{eg}(N_{eg} - N_{oeg})} = a_{eg} h_{eg} N_{0eg} e^{-a_{eg}(t - h_{eg} N_{0eg} - h_{ig}(N_{0ig} - \frac{w(a_{eg} h_{ig} N_{0ig} e^{-a_{eg}(t - h_{ig} N_{0ig} - h_{eg} N_{eg})})}{a_{ig} h_{ig}}))} \tag{A6}$$

By simplification:

$$-(N_{eg} - N_{0eg}) e^{-a_{eg} h_{eg} N_{eg}} = N_{0eg} e^{-a_{eg}(t - h_{ig}(N_{0ig} - \frac{w(a_{eg} h_{ig} N_{0ig} e^{-a_{eg}(t - h_{ig} N_{0ig} - h_{eg} N_{eg})})}{a_{ig} h_{ig}}))} \tag{A7}$$

$$-(N_{eg} - N_{0eg}) e^{-a_{eg} h_{eg} N_{eg}} = N_{0eg} e^{-a_{eg}(t - h_{ig} N_{0ig})} e^{-w(a_{eg} h_{ig} N_{0ig} e^{-a_{eg}(t - h_{ig} N_{0ig} - h_{eg} N_{eg})})} \tag{A8}$$

Given that $e^{w(x)}w(x) = x$ and $e^{-w(x)} = \frac{w(x)}{x}$, Eq. A8 is equal to:

$$-(N_{eg}-N_{0eg})e^{-a_{eg}h_{eg}N_{eg}} = N_{0eg}e^{-a_{eg}(t-h_{ig}N_{0ig})}w(a_{eg}h_{ig}N_{0ig}e^{-a_{eg}(t-h_{ig}N_{0ig}-h_{eg}N_{eg})})\frac{e^{a_{eg}(t-h_{ig}N_{0ig}-h_{eg}N_{eg})}}{a_{eg}h_{ig}N_{0ig}} \quad \text{(A9)}$$

By simplification:

$$-(N_{eg}-N_{0eg})a_{eg}h_{ig}\frac{N_{0ig}}{N_{0eg}} = w(a_{eg}h_{ig}N_{0ig}e^{-a_{eg}(t-h_{ig}N_{0ig}-h_{eg}N_{eg})}) \quad \text{(A10)}$$

Given that $w^{-1}(x) = xe^{x}$, Eq. A10 is equal to:

$$-(N_{eg}-N_{0eg})a_{eg}h_{ig}\frac{N_{0ig}}{N_{0eg}}e^{-(N_{eg}-N_{0eg})a_{eg}h_{ig}\frac{N_{0ig}}{N_{0eg}}} = a_{eg}h_{ig}N_{0ig}e^{-a_{eg}(t-h_{ig}N_{0ig}-h_{eg}N_{eg})} \quad \text{(A11)}$$

By simplification:

$$-\frac{(N_{eg}-N_{0eg})}{N_{0eg}}e^{-N_{eg}a_{eg}h_{ig}\frac{N_{0ig}}{N_{0eg}}} = e^{-a_{eg}(t-h_{eg}N_{eg})} \quad \text{(A12)}$$

Then:

$$-\frac{(N_{eg}-N_{0eg})}{N_{0eg}}e^{-N_{eg}a_{eg}(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg})} = e^{-a_{eg}t} \quad \text{(A13)}$$

Then:

$$-a_{eg}(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg})(N_{eg}-N_{0eg})e^{-(N_{eg}-N0eg)a_{eg}(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg})} = a_{eg}(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg})N_{0eg}e^{-a_{eg}t+N_{0eg}a_{eg}(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg})} \quad \text{(A14)}$$

Applying *w* to each side yields:

$$-a_{eg}(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg})(N_{eg}-N_{0eg}) = w(a_{eg}(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg})N_{0eg}e^{-a_{eg}t+N_{0eg}a_{eg}(h_{ig}\frac{N_{0ig}}{N_{0eg}}+h_{eg})}) \quad \text{(A15)}$$

Then:

$$N_{eg} = N_{0eg}(1-\frac{w(a_{eg}(h_{ig}N_{0ig}+h_{eg}N_{0eg})e^{-a_{eg}(t-h_{ig}N_{0ig}-h_{eg}N_{0eg})})}{a_{eg}(h_{ig}N_{0ig}+h_{eg}N_{0eg})} \quad \text{(A16)}$$

And:

$$N_{eg}+N_{ig} = (N_{0eg}+N_{0ig})\times(1-\frac{w(a_{eg}(h_{eg}N_{0eg}+h_{ig}N_{0ig})\times e^{-a_{eg}(t-h_{eg}N_{0eg}-h_{ig}N_{0ig})})}{a_{eg}(h_{ig}N_{0ig}+h_{eg}N_{0eg})}) \quad \text{(A17)}$$