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REVIEW

Effect of crop diversity on predation activity and population dynamics of the mirid predator *Nesidiocoris tenuis*

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Abstract
A considerable body of evidence has demonstrated the positive impact of the diversity of plant species on biological control of pests at the field scale. However, very few studies have assessed the effect of crop diversity on natural enemy performance and pest control. In order to test our hypothesis that crop diversity could increase natural enemy development and performance, we examined the mechanisms underlying the effect of two types of crop succession, i.e., multiple-crop succession (tomato, squash and soybean) and mono-crop succession (each crop alone), on population dynamics, predation capacity and spillover of *Nesidiocoris tenuis* Reuter (Hemiptera: Miridae) in a greenhouse experiment. We found that (1) the polyculture supported lower population growth of *N. tenuis* and lower predation rates of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs compared to tomato and squash monocultures, but that correspondingly (2) the predator performed better on the polyculture than on the soybean monoculture. These results revealed that crop identity within the succession is a major factor in determining population dynamics and biological control. We found that compared to soybean monoculture, the presence of soybean *Glycine max* L. (Fabales: Fabaceae) in the polyculture treatment reduced the population dynamics of the mirid predator but increased biological control. This result suggests that non-host crops in a polycultural succession could benefit from the natural enemy populations that were increased by other suitable crops in the succession.

Keywords Habitat management · Crop succession · Conservation biological control · Predation · Spillover

Key messages

- *Nesidiocoris tenuis* performed better on the polyculture than on the soybean monoculture.
- Polyculture supported lower population growth of *N. tenuis* and predation of *Ephestia kuehniella* eggs compared to tomato and squash monocultures.
- Crop identity has a major effect on population dynamics of *N. tenuis* and biological control.
- Non-host crops in a polycultural succession can contribute to biological control.

Introduction

Modern industrial agriculture has a considerable negative environmental impact, such as the side effects of pesticides on beneficial arthropods, habitat fragmentation, diversity loss, threatening the sustainability of most food production systems (Kareiva 1987; Desneux et al. 2007; Lu et al. 2012; Jonsson et al. 2014; Wood and Goulson 2017; Seibold et al. 2019; Taiwo 2019). Ecological intensification offers a way of reducing this environmental impact by improving ecological processes in agroecosystems and limiting agrochemical dependency (Letourneau et al.

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2015). Among the approaches used in ecological intensification, conservation biological control, based on the use of locally present natural enemies to reduce pest populations, is an important ecosystem service that can help to reduce pesticide use and crop damage (Parolin et al. 2012; Heimpel and Mills 2017; Zhao et al. 2017; Karp et al. 2018; Perovic et al. 2018).

Key resources such as pollen, nectar, nesting sites and alternative hosts and prey within agricultural landscapes are known to have a major impact on natural enemy population dynamics (Gurr et al. 2017; Perovic et al. 2018; Desneux et al. 2019). Enhancing plant diversity to maintain multiple resources, either in the field or at the landscape level, could boost natural enemy populations and reduce pest infestation levels (Lundgren et al. 2009; Letourneau et al. 2011; Bianchi et al. 2006; Rusch et al. 2016; Karp et al. 2018; Gurr et al. 2017; Hatt et al. 2019). A diversity of resources targeting all natural enemy life stages and the spatiotemporal continuity of those resources in agricultural landscapes are crucial elements in maintaining natural enemy populations throughout the year (Schellhorn et al. 2015). At the landscape level, the study of the effect of plant diversity on natural enemies often compares the proportion of semi-natural habitats (i.e., habitat complexity) and the proportion of cultivated areas (Rusch et al. 2016; Karp et al. 2018; Gurr et al. 2017) without taking into account the potential effect of crop diversity on natural enemies.

However, increasing plant diversity through semi-natural habitats can be costly in terms of space and management for farmers. In a context of increasing demand for food, extensive growth of urban surfaces and reduced agricultural intensification, increasing semi-natural areas in agricultural landscapes seems difficult to implement (Bianchi et al. 2006; Burton et al. 2008; Brewer and Goodell 2012). Playing on crop diversity as a way to provide key resources to natural enemies is a complementary approach that could be easier to implement. This approach would certainly provide direct value to farmers and thus might well encourage them to adopt such systems (Vasseur et al. 2013). Crops can provide high amounts of a specific resource (nectar, pollen or alternative hosts/prey), but only during a brief period in conventional agricultural systems (Rand et al. 2006; Tscharntke et al. 2005). Associating crops to provide continuous and complementary resources for natural enemy populations could increase biological control of pests (Letourneau et al. 2011; Vasseur et al. 2013; Schellhorn et al. 2015). Such systems would require a thorough understanding of the quality and temporality of the resources provided by each crop, as well as the precise needs of the targeted natural enemies (Schellhorn et al. 2015). Also, they should allow natural enemies to spill over from one crop to another thanks to minimized distance between crops and temporal resource overlaps (Rand et al. 2006). Understanding the mechanisms underlying the effect of crop diversification on the biological control of pests is essential for successful cropping design.

Predatory mirids are natural enemies often used in biological control programs and are a key pest control strategy currently used in the Mediterranean basin on tomato and sweet pepper crops (Perdikis et al. 2011; Jaworski et al. 2015; Pérez-Hedo and Urbaneja 2015; Mansour et al. 2018). Mirids are known to be omnivores, feeding on different types of prey (e.g., whiteflies, lepidopteran larvae, soft bodied insects, etc.) and on plant materials (mainly tomato, cotton, Cucurbitaceae in general, gerbera) (Castañé et al. 2011; Bompard et al. 2013; Jaworski et al. 2013; Han et al. 2015a; Jiao et al. 2019; Li et al. 2020). Many studies have shown that mirid predators can be found on many different types of host plants, mainly Solanaceae, Asteraceae, Cucurbitaceae, Fabaceae and Pedaliaceae (Naselli et al. 2017; Biondi et al. 2016; Sánchez et al. 2003). *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae) is a mirid predator largely used in greenhouses as it has the capacity to feed on many different types of key pests. This species feeds on both plant sap, pollen, nectar and soft bodied insects or eggs (Calvo et al. 2009; Arnó et al. 2010; Molla et al. 2014), thus making it an ideal candidate in the investigation of the effects of plant diversification on biological control. It has particularly been studied for its capacity to control the tomato leaf miner *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Desneux et al. 2010; Biondi et al. 2018) and the whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) (Calvo and Urbaneja 2004), but also aphids on pepper plants (Pérez-Hedo and Urbaneja 2015). Despite the propensity of the mirid predator to cause necrotic rings on plant stems, new studies have found that by manipulating tomato varieties or temperatures, the damage caused by the predator could be reduced, thus making it a good candidate for biological control in greenhouses (Siscaro et al. 2019). Additionally, the plant defenses induced by the mirid predator could also benefit other associated plants in the succession and reduce pest pressure on the crops (Pérez-Hedo and Urbaneja 2015).

This study aims at analyzing the effect of crop richness and continuous crop succession on the population growth, the predation capacity and the spillover of the mirid predator *Nesidiocoris tenuis* Reuter. Increasing crop species richness over space and time might lead to: (1) a higher population growth of the natural enemy, (2) enhanced predation efficiency of *N. tenuis*, (3) a higher spillover of predators compared to monocultural systems.

Materials and methods

Biological materials

Predatory mirid

The predator studied in this experiment is the mirid predator *N. tenuis* Reuter. The mirid predator colony was reared on tomato plants under laboratory conditions (25 ± 3 °C; LD 15:9; 50 ± 10% RH). The colony was regularly fed with sterilized *E. kuehniella* Zeller (Lepidoptera: Pyralidae) eggs (Biotop$^{®}$, Livron-sur-Drôme, France), honey diluted in water (1/4) and commercial pollen grains from diverse types of flowers.

Prey

Sterilized *E. kuehniella* eggs were used as substitute prey during the whole study (Han et al. 2015a, b, 2020). Other Pyralidae species are important pests in many agricultural systems, making *E. kuehniella* a good representative of this type of pest. Only sterilized eggs were used for the experiment in order to simplify the trophic system and focus on the direct effects on the natural enemy of plant diversity and succession.

Plants

Three different plant species were chosen for the experimental design: tomato (*Solanum lycopersicum* L. (Solanaceae)—Nano), squash (*Cucurbita moschata* D. (Cucurbitaceae)—Butternut) and soybean (*Glycine max* L. (Fabaceae)—Merrill). These plants were chosen because they are complementary in terms of: (1) botanical family and (2) provision of nectar and pollen (see Table 1). Pretests were done in order to confirm that the mirid predator is able to grow on the different plants selected. During the experiment, all plants reached the flowering stage, allowing the predatory mirid to feed on pollen and nectar sources when available in addition to sap collected mainly on the apical vegetative sprouts (Siscaro et al. 2019) and to *E. kuehniella* eggs available on predation cards.

Experimental design

The experiment was carried out under greenhouse conditions from May 17 to July 27, 2017, at the INRAe site in Sophia Antipolis. The temperature and the relative humidity were stabilized using cooling and fogging systems (25 ± 10 °C; 15L:9D ± 1 h as photoperiod; 70 ± 20% RH). The experimental greenhouse was composed of four hermetically separated compartments, each measuring 6 × 6 m. In each compartment, four double rows of metal poles each measuring 5 m long were placed as a support for the plants. A nutritive solution elaborated at INRAe and provided four times a day to all the plants in the experiment was used ($NO_3 = 1$; $H_2PO_4 = 0.21$; $SO_4 = 0.055$; $K = 0.641$ $Ca = 0.215$; $Mg = 0.114$) (Han et al. 2014, 2016).

Treatments

To look into the effects of crop diversity on *N. tenuis*, the succession of three crops, hereafter named "polyculture," was compared to the succession of the same crop for each crop separately, hereafter named "monocultures" (Table 1 and Fig. 1). Consequently, there were four treatments: the tomato monoculture, the squash monoculture, the soybean monoculture and the polyculture. Each treatment was replicated four times, once in each compartment. A replicate

Table 1 Description of plant succession in time and space

<table>
<tr><td rowspan="3"></td><td colspan="11">Patch type A</td><td colspan="13">▨</td></tr>
<tr><td colspan="6">▨</td><td colspan="12">Patch type B</td><td colspan="6">▨</td></tr>
<tr><td colspan="13">▨</td><td colspan="11">Patch type C</td></tr>
<tr><td rowspan="3">Polyculture</td><td colspan="11">Tomato</td><td colspan="13">▨</td></tr>
<tr><td colspan="6">▨</td><td colspan="12">Squash</td><td colspan="6">▨</td></tr>
<tr><td colspan="13">▨</td><td colspan="11">Soybean</td></tr>
<tr><td rowspan="3">Tomato monoculture</td><td colspan="11">Tomato</td><td colspan="13">▨</td></tr>
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<tr><td colspan="13">▨</td><td colspan="11">Tomato</td></tr>
<tr><td rowspan="3">Squash monoculture</td><td colspan="11">Squash</td><td colspan="13">▨</td></tr>
<tr><td colspan="6">▨</td><td colspan="12">Squash</td><td colspan="6">▨</td></tr>
<tr><td colspan="13">▨</td><td colspan="11">Squash</td></tr>
<tr><td rowspan="3">Soybean monoculture</td><td colspan="11">Soybean</td><td colspan="13">▨</td></tr>
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<tr><td colspan="13">▨</td><td colspan="11">Soybean</td></tr>
<tr><td>Day</td><td colspan="2">1</td><td colspan="2">5</td><td colspan="2">10</td><td colspan="2">15</td><td colspan="2">20</td><td colspan="2">25</td><td colspan="2">30</td><td colspan="2">35</td><td colspan="2">40</td><td colspan="2">45</td><td colspan="2">50</td><td colspan="2">55</td></tr>
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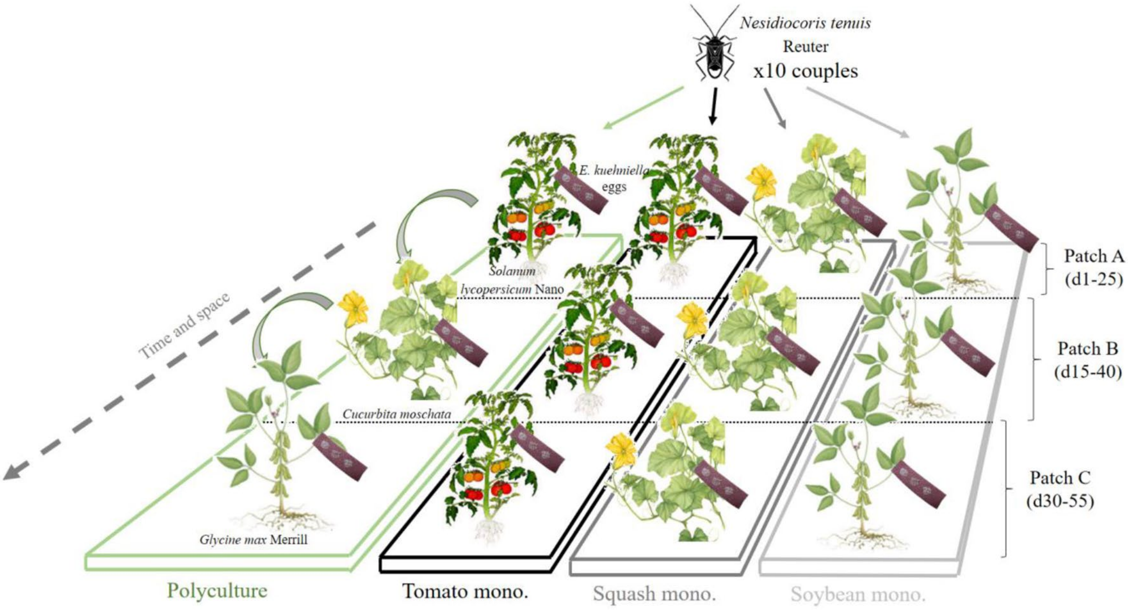

Fig. 1 Representation of the greenhouse experimental design. One row represents one tunnel and one treatment (polyculture, monocultures of tomato, squash and soybean). The patch types are represented in time and space. Plants in patch A were let from day 1 to day 25, plants in patch B were let from day 15 to day 40, and plants in patch C were let from day 30 to day 55. Each tunnel was separated by means of mesh nets. Each treatment was replicated 4 times in the entire greenhouse

consisted of a double row of plants, isolated from the others by means of a net tunnel. The effect of plant succession on natural enemy spillover was assessed using the following design: Each double row of plants was divided into three equal parts representing a unit of space and time called "patch type" in which 8 plants were placed: A, B and C (Table 1 and Fig. 1). In the polyculture treatment, the plants in patch type A were tomato plants, squash plants were in patch type B and soybean plants in patch type C. In the monoculture treatments, all patch types contained the same crop. The patch types of plants were added gradually, every 15 days. Nevertheless, in order to assess the effect of habitat disturbance in the system, each plant patch type was cut 25 days after its implementation, and the crop residues were left to allow potential *N. tenuis* offspring to develop. In brief, after implementing plants in patch type A, on day 15 patch type B was added; then, on day 25, patch type A was cut, on day 30, patch type C was added, and on day 40, patch type B was cut. Thanks to this technique, the insects always had 10 days to switch from one patch type to another.

Predator population dynamics and spillover between the patch types

On day one, 10 three-day-old *N. tenuis* females and 10 three-day-old *N. tenuis* males were placed in each treatment. The *N. tenuis* populations were sampled in each tunnel every 5 days. Insects were counted on the living plants, on plant residues as well as in the environment nearby. In order to avoid any overlapping during the insect sampling, each individual was lifted out carefully using a mouth aspirator in each patch and then put back in the middle of the same patch at the end of the counting. All instars were noted, i.e., nymphal instars 1, 2, 3, 4 and 5 and male and female adults. To assess the spillover of the predators, evaluated as the movement of the predatory mirids from one patch type to another, the patch types were physically separated by a net during the sampling in order to avoid any movement of the predators from one patch to another induced by the disturbance of the sampling. The position of the individuals was then recorded in each patch type. Population spillover was assessed by calculating the percentage of the population present in a patch type, compared to the previous patch type, based on the formula below:

$$\frac{\text{Number of insects in Patch type } X \text{ at time } t * 100}{\text{Number of insects in Patch type } (X-1) \text{ at time } t}$$

The spillover was also assessed through the comparison of the population of *N. tenuis* between the patch types within a treatment. Patch types represent a unit of space and as such provide a good basis to measure the movement intensity of the population. We assumed that population abundance might vary between the patch types depending on the plants available in the system.

Predation performance

Predation cards made with *E. kuehniella* sterilized eggs were used to estimate *N. tenuis* predation performance (Winqvist et al. 2011). The quantity of eggs exposed to mirid predators was based on the results from preliminary experiments. In the greenhouse, predation cards were disposed homogenously on the living plants and were replaced every 2 days to avoid dehydration or total predation. Firstly, every other day, eight predation cards per patch type were installed, with approximately 600 eggs each; from day 12 on, when the second generation of *N. tenuis* appeared, 16 cards were installed. As predated eggs and dehydrated eggs were difficult to distinguish, control cards protected by a small bag made of nylon mesh were also placed in the tunnels in order to measure a mean dehydration rate per compartment on each date. The number of predated eggs per patch type was estimated every 2 days by counting damaged eggs using a binocular magnifying lens, and the mean dehydration rate was suppressed. The mean number of predated eggs per insect per day was also calculated. The predation per insect per day was only calculated on tomato and squash monocultures and on polyculture, as the number of individuals was too low in soybean monoculture to establish the metric (less than 5 individuals on average in patches B and C). The population in patch type C was not high enough to calculate the mean number of predated eggs until day 41 as *N. tenuis* individuals did not transfer to the last patch type in polyculture. Therefore, the predation per insect per day was only compared in patch type C from day 41 to the end of the experiment.

Statistical analysis

The effects of the different treatments on *N. tenuis* population and predation performance (number of predated eggs) were analyzed using generalized estimating equations (GEEs) with a Poisson error distribution. Each model used the patch type and the date separately and their interactions as explanatory variables. We specified a first-order auto-regressive correlation structure "ar1," based on the assumption that observations close in time are much more correlated than observations further apart. The GEE model was simplified using a backward stepwise method. The post hoc test "lsmeans" (Lenth 2016) was used for mutual comparison of the treatments.

The spillover of the predator population was analyzed using a generalized linear model (GLM) with a Poisson error distribution. The variables used to explain the total number of predators were the treatment and the patch type in interaction. Spillover was considered effective when the patch type significantly impacted the population of *N. tenuis*; it is considered as a unit of space and time. A population significantly different in the different patches therefore demonstrates a movement from one patch to another in time and in space.

All statistical analyses were carried out using the R software v3.5.1 using the geepack package (Højsgaard et al. 2006), the lsmeans package (Lenth 2016) and the multcomp package (Hothorn et al. 2008).

Results

Population dynamics

In the soybean monoculture compared to the polyculture and the tomato and squash monocultures, the number of *N. tenuis* was significantly lower (Table S1; soybean–squash: z.ratio: -15.1, $P<0.001$; soybean–tomato: z.ratio: -13.5, $P<0.001$; soybean polyculture: z.ratio: -11.6, $P<0.001$). The lower population of predator in soybean monoculture was checked in each patch type (Fig. 2, Table S2; all $P<0.001$) with the initial adult population in soybean dropping from the beginning of the experiment. The abundance of *N. tenuis* in the polyculture was equal to the tomato and squash monocultures in patch type A and B (Table S2; all $P>0.05$), whereas in patch type C, the number of *N. tenuis* was significantly lower in the polyculture (Fig. 2; Table S2; squash polyculture in patch type C: z.ratio: 5.2, $P<0.001$; tomato polyculture in patch type C: z.ratio: 4.8, $P<0.001$). There was no difference in the number of *N. tenuis* between tomato and squash monocultures in either of the patch types (Table S2; all $P>0.05$).

Population spillover

As well as in the patch type, the treatment had a significant effect on the number of *N. tenuis* (Table S3; treatment: $\chi^2{}_1$: 854.1, $P<0.001$; patch type: $\chi^2{}_2$: 2024.95, $P<0.001$). The spillover, measured as a percentage of population transfer from one patch type to another, could not be calculated on the soybean monoculture as too few insects were present. In the tomato and the squash monocultures, the population transfer was identical from patch type A to patch type B and from patch type B to patch type C, i.e., 50% of the population transferred within 8 days and 90% within 14 days (Fig. 3). In the polyculture and in the monocultures, the population transfer was constant from patch type A to patch type B, i.e., from the tomato to the squash patch type in polyculture. Nevertheless, the transfer was much slower from patch type B to patch type C in polyculture, namely from the squash to the soybean patch type, i.e., after 8 days following the cutting of the plant, only 14% of the insects transferred to the soybean patch type (Fig. 3).

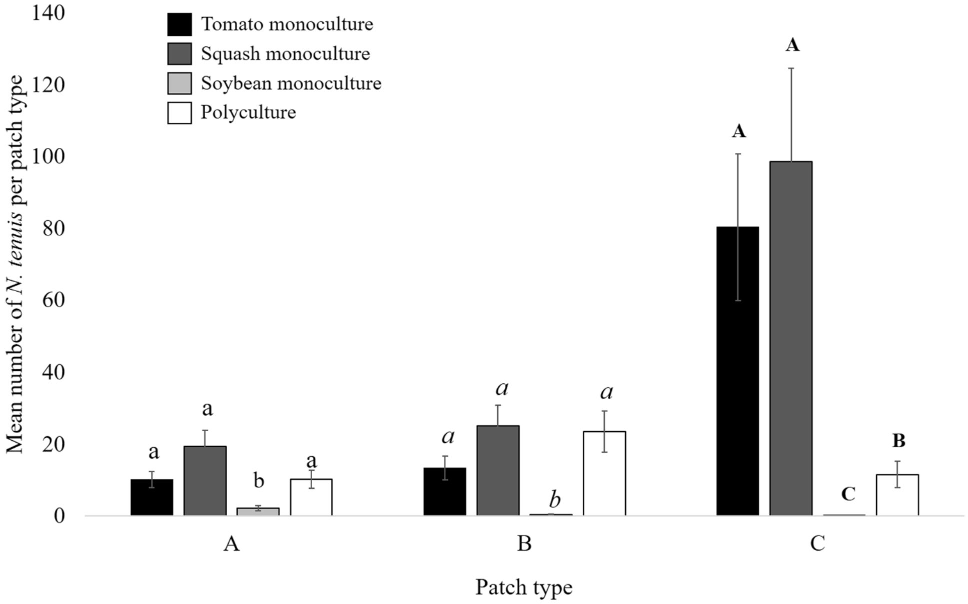

Fig. 2 Mean *N. tenuis* population size (mean ± SEM) per patch type (A, B, C) in the three monoculture and the polyculture treatments. In the polyculture, the plant in patch type A is tomato, in patch type B, squash and in patch type C, soybean. Bar charts bearing different letters, i.e., in normal, italic or capital letters, differ significantly at $P < 0.05$ (GEE analysis)

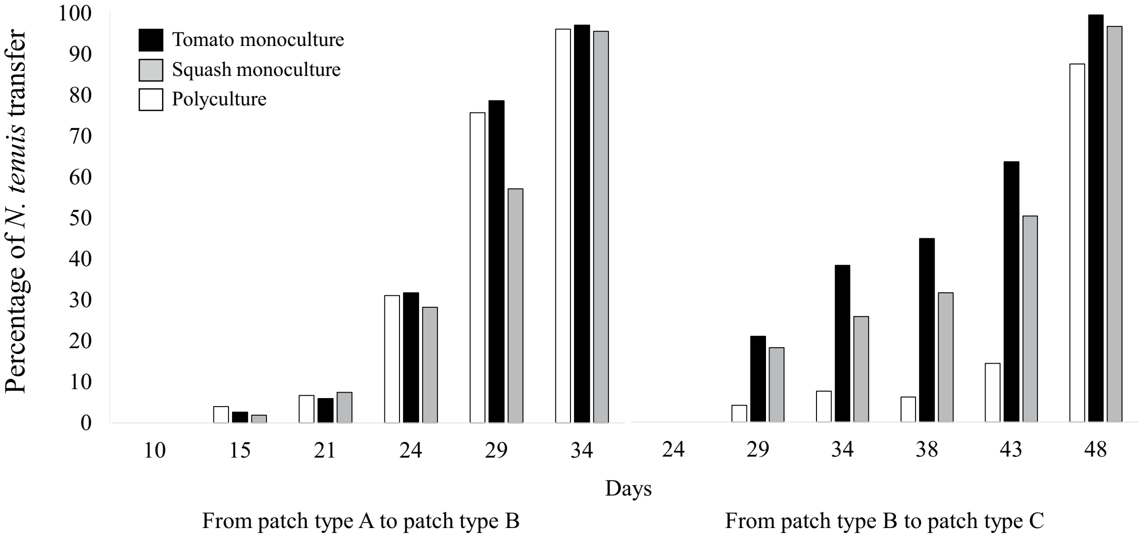

Fig. 3 Percentage of transfer of the *N. tenuis* population from patch type A to patch type B, on the left part of the graph, and from patch type B to patch type C on the right part of the graph, after cutting the plant in patch type A on day 25 and patch type B on day 40

Predation performance

The treatment significantly impacted the number of predated eggs, with a predation in the squash monoculture significantly higher in every patch type during the entire period (Fig. 4, Table S4 and S5; χ^2_3: 291.9, $P < 0.001$). On patch type A, predation was similar in the polyculture, the tomato monoculture and the soybean monoculture. Predation in the polyculture was equal to predation in the tomato monoculture in patch type B and was lower in patch type C (Fig. 4; tomato polyculture: z.ratio: −2.5, $P = 0.056$; tomato polyculture: z.ratio: 5.6, $P < 0.001$). Predation in the polyculture was higher than in the soybean monoculture in patch type B and C (Fig. 4; soybean polyculture: z.ratio: −4.03, $P < 0.001$; soybean–tomato: z.ratio: −9.5, $P < 0.001$).

Predation per insect per day could only be calculated in patch types B and C in the polyculture and tomato and squash monocultures as at the beginning of the experiment, the number of adults dropped to levels excluding the calculation of the metric (from 10 to 20 individuals on average). No significant difference was observed between the treatments on patch type B. In patch C, from day 41 to day 47, the mean number of predated eggs per insect per

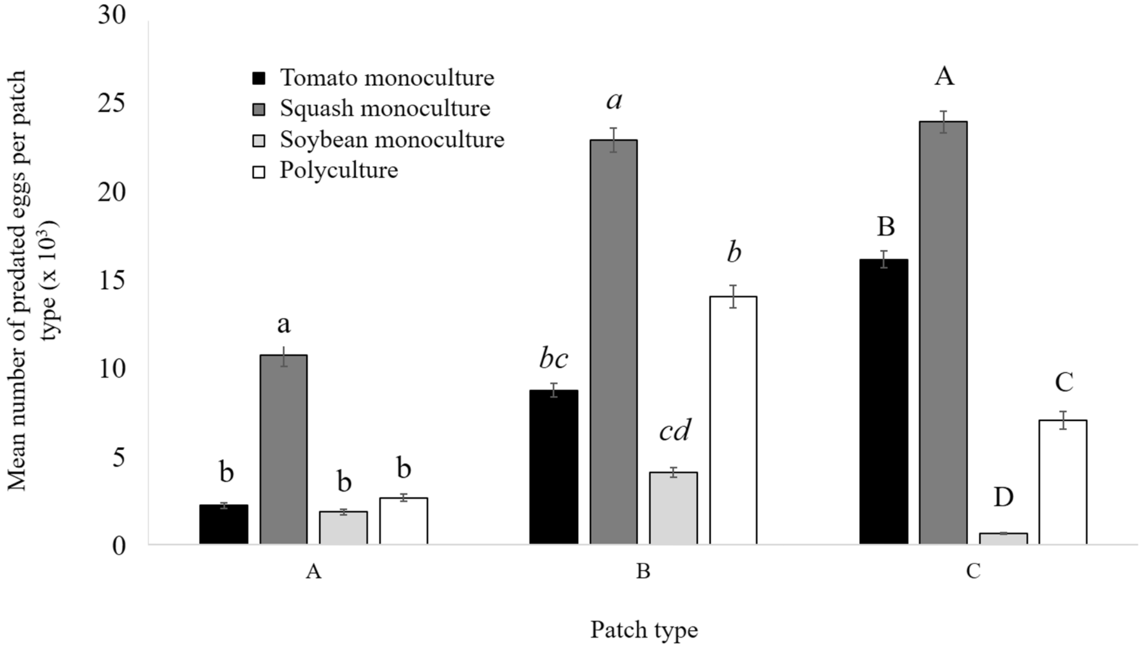

Fig. 4 Mean number of predated eggs by *N. tenuis* (mean ± SEM) per patch type (A, B, C) in the three monoculture and the polyculture treatments. In the polyculture, the plant in patch type A is tomato, in patch type B, squash and in patch type C, soybean. Bar charts bearing different letters, i.e., in normal, italic or capital letters, differ significantly at $P < 0.05$ (GEE analysis)

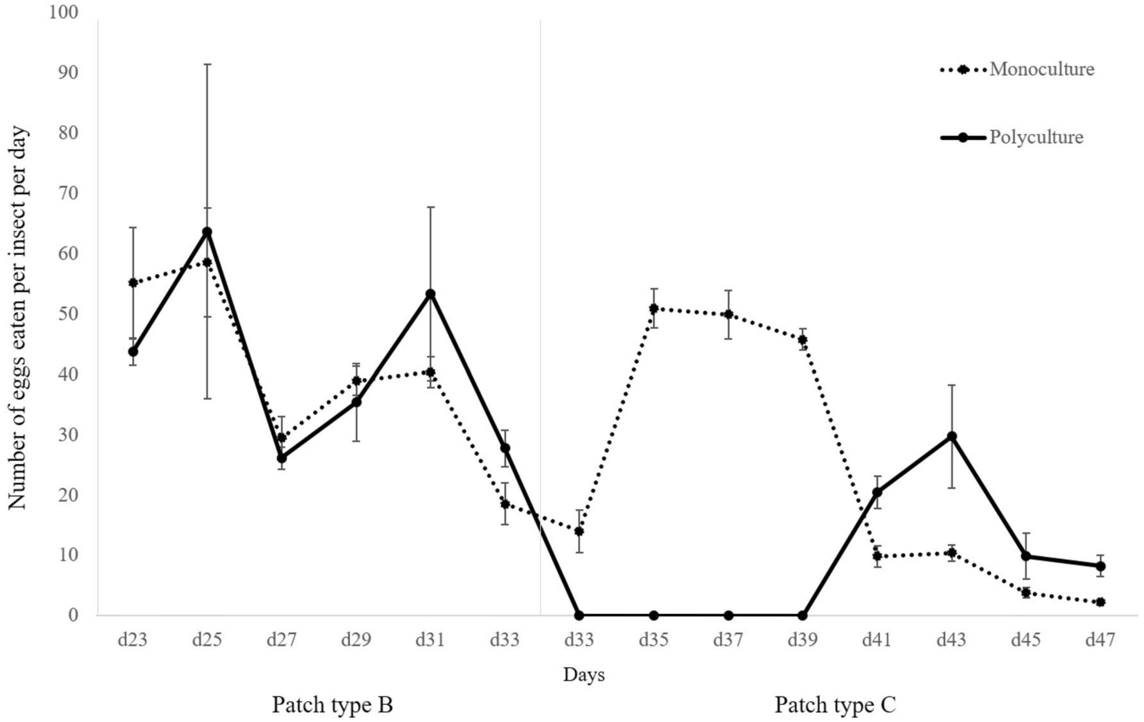

Fig. 5 Number of eggs eaten per insect per day (mean ± SEM) in the combined monoculture treatments and the polyculture treatment. In the polyculture, the plant in patch type B is squash and in patch type C, soybean. The data in polyculture from day 33 to day 39 were taken out of the graph as the number of individuals was lower than 10

day was significantly higher in the polyculture than in the monocultures tomato and squash combined (Fig. 5; $\chi^2{}_1$: 14.6, $P<0.001$). When comparing the different treatments during the overall period, predation per insect per day in the squash monoculture was higher than in the tomato monoculture (Table S5; squash–tomato: z.ratio: 3.5, $P=0.001$). Predation did not differ among the other treatments (Table S5; squash polyculture: z.ratio: 0.7, $P=0.72$; tomato polyculture: z.ratio: -1.8, $P=0.15$).

Discussion

A highly diverse plant community is likely to provide more abundant and diversified resources to higher trophic levels than a low diversified plant community. Our study assessing the effect of the richness of crop species on *N. tenuis* ability to control pests shows interestingly that the predator relies more on the plant species than on the richness of the resources, as demonstrated for other mirids (Biondi et al. 2016; Balzan 2017). Our analyses revealed that the performance and the population dynamics of this omnivorous predator were quite stable in all monocultures and varied in the polyculture with regard to the plant to which it was exposed. Our results suggest that contrary to our initial hypothesis, increasing crop diversity per se is not sufficient to enhance biological pest control services in agricultural landscapes (Koricheva et al. 2000).

In polyculture, the three crops were combined to provide continuous and diversified food sources. The weaker development of *N. tenuis* population in the polyculture compared to the tomato and squash monocultures may be explained by the presence of the soybean patch type at the end of the experimental period, i.e., patch type C, as it was probably poorly suitable for *N. tenuis* development (see below). Mirids are zoophytophagous arthropods and therefore need plants and prey for their development. Apart from feeding, the mirids also need the plant for oviposition which makes the quality of the plant crucial for their development (Coll 1996; Biondi et al. 2016). The population of the predatory mirid decreased at the end of the experiment in patch type C because the cutting of squash crop led to the death of the third generation of newly emerged adults unable to lay their eggs in the soybean patch. It might also be possible that the effects of crop diversity on natural enemy populations were not observable after a succession of only two crops as landscape heterogeneity may have long-term or lag effects on natural enemy populations (Gurr et al. 2017).

The delayed spillover of the insects from squash to soybean in the polyculture compared to the monocultures shows that soybean plants do not attract *N. tenuis*. This resulted in a lower predation efficiency observed in the last patch type of the polyculture compared to the squash and tomato monocultures. Therefore, if the plant available in a cropping system is not adapted to the development of the targeted natural enemy and is less attractive than other crops in the surroundings, the natural enemy will barely transfer to it and thus will not provide biological control services. The surroundings of a crop play an important role in the spillover of natural enemies as shown with parasitoids (Inclán et al. 2015). However, despite the unattractiveness of soybean, the insects finally transferred when squash residues had completely dried out, probably to find other food sources (Han et al. 2015a; Pan et al. 2014). In fact, predation in the soybean patch type in the polyculture was much higher than in the soybean monoculture, showing that in the polyculture, the soybean benefited from the previous population increase in the tomato and the squash patches. These findings support the idea that implementing a “bridge crop” inside a crop succession design may enhance biological control, a phenomenon that has already been shown in natural habitats adjacent to crops (Rand et al. 2006). When a crop does not fulfill all the needs of the main targeted predators, it could benefit from a high level of biological control thanks to the spillover of predators from other crops within the system.

Other factors not taken into consideration in this study might attract natural enemies to a patch of crops. For example, *N. tenuis* is attracted by HIPVs (herbivore-induced plant volatiles) produced by plants infested by the whitefly *Bemisia tabaci* Gennadius and the tomato borer *Tuta absoluta* Meyrick (Lins et al. 2014). In this experiment, plants were not exposed to herbivory as the pest was replaced by sterilized eggs of *E. kuehniella*. *Nesidiocoris tenuis’* foraging behavior and spillover from one patch type to another might thus have been different with a live pest.

The results of this study demonstrate how the choice of the plant can impact the population of *N. tenuis*, not only in its overall population growth but also in its foraging behavior and its predation capacity. Furthermore, as the population grew, the number of predated eggs increased, stressing at the importance of maintaining a stable natural enemy population in crops in order to profit from their activity (Gurr et al. 2017). Multiple factors could explain the unsuitability of the soybean plant. First of all, the poor water resource given by the young soybean plant may have hindered nutrition of *N. tenuis* individuals, as the species’ main food resource is sap (Sánchez et al. 2006). Moreover, the lack of water in plant tissue could increase the hardness of plant tissue and could therefore affect the possibility for *N. tenuis* of laying eggs as they are deposited by endophytic oviposition, placing the eggs inside the plant tissue (De Puysseleyr et al. 2013; Lundgren et al. 2008; Constant et al. 1996). The percentage of dry matter in the soybean tissue was indeed much higher compared to squash and tomato. However, another study has shown that *Macrolophus pygmaeus* (Hemiptera: Miridae), a similar predatory mirid with the same needs as *N. tenuis*, developed well on the green pea (*Pisum sativum*, L.), which belongs to the same family, and has the same morphology as the soybean plant, excluding other food sources (Perdikis and Lykouressis 2000). The development of the two mirid predators might differ on these two plants due to the morphology and accessibility of the flower to the mirid predator. Finally, the low biomass represented in the soybean plant rows may have prevented the mirid predator from installing therein. Biomass is an important functional trait for the maintenance of natural enemies in a field (Gardarin et al. 2018; Honek and Jarošík 2000).

Squash and tomato monocultures considerably encouraged the development of *N. tenuis*, and predation in these treatments proved to be effective. It is worth mentioning that although the number of insects was the same in both monocultures, predation capacity was significantly higher in the squash monoculture. One explanation may be that the need of *N. tenuis* for other food sources, notably eggs, is reduced in the tomato monoculture by its capacity to feed on tomato sap, as the tomato is its main host plant. We note that predatory mirids can feed on plant sap only if the host plant is suitable (Perdikis and Lykouressis 2000; Perdikis and Arvaniti 2016). A second hypothesis is that pollen and nectar provided by squash are more readily available for *N. tenuis* in terms of quantity, quality and accessibility than on tomato plants. As some studies have shown that plant food could enhance the performance of *N. tenuis* (Maselou et al. 2015) and increase the feeding activity of other mirid species (Han et al. 2015a), it could be suggested that squash bolstered *N. tenuis* predation capacity by providing complementary food sources.

Conclusion and perspectives

Our study demonstrates that crop identity is crucial when designing cropping systems to improve biological control services based on crop diversification. The predator performed much better on polyculture than on soybean monoculture, whereas it was less effective on polyculture compared to squash and tomato monocultures. It is interesting to note that at the end of the experiment, when the predator population spilled over to the soybean crop in the polyculture, predation efficiency increased and was significantly higher than in the combined monocultures. These results suggest that non-host crops in a cultural succession can benefit from the presence of host plants that support the targeted natural enemy. These findings infer that implementing a ‘bridge’ crop is possible in crop succession design even if less suitable for the targeted natural enemy. In future studies, more attention should be given to analyse the effect of plant types on natural enemies. Since natural enemies have different life history traits, the selection of the crops included in a diversified cropping system should be taken into account in the management of the natural enemy populations. A functionally diversified cropping system could support a diversity of natural enemies, each species being more or less enhanced by certain crops. Further studies are thus required to implement a polycultural cropping system that would favor biological control through crop diversity by taking into account the complexity of natural enemy communities (Gardarin et al. 2018).

Author contributions

EJ, ND and ET designed the experiment. EJ, ET and PB performed the bioassays. ND provided technical and material supports. EJ, ET and AR analyzed the data. ET, EJ and AR led the writing of the manuscript, and all authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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