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Host-mediated, cross-generational intraspecific competition in a multivoltine herbivore species

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Conspecific insect herbivores co-occurring on the same host plant interact both directly through interference competition and indirectly through exploitative competition, plant-mediated interactions and enemy-mediated interactions. However, the situation is less clear when the interactions between conspecific insect herbivores are separated in time within the same growing season, as it is the case for multivoltine species. We hypothesized that early season herbivory would result in reduced egg laying and reduced performance of the next generation of herbivore on previously attacked plants. We tested this hypothesis in a choice experiment with box tree moth females, *Cydalima perspectalis* Walker (Lepidoptera: Crambidae), to which box trees, *Buxus sempervirens* L. (Buxaceae), were proposed that had or had not been previously defoliated by BTM larvae earlier in the season. We then compared the performance of the next generation larvae on previously damaged *vs* undamaged plants. Previous herbivory had no effect on oviposition behaviour, but the weight of next generation larvae was significantly lower in previously damaged plants. There was a negative correlation between the number of egg clutches per plant and larval performance. Overall, our findings reveal that early season herbivory reduces the performance of conspecific individuals on the same host plant later in the growing season, and that this time-lagged intraspecific competition results from a mismatch between the oviposition preference of females and the performance of their offspring.

1 Introduction

Insect herbivores exploiting the same plant can compete for food, even when interactions among individuals are separated in time (Kaplan & Denno, 2007). Insects may thus reduce the impact of inter- and intraspecific competition by avoiding crowded plants, or plants that have been previously consumed by herbivores, which supposes that they can detect competitors or their effects on plants (De Moraes et al., 2001; Shiojiri & Takabayashi, 2003). For many species, the choice of the oviposition site by mated females is crucial in this respect. The preference-performance hypothesis - *aka* the '*mother knows best hypothesis*' - states that female insects evolved host searching behaviour that leads them to oviposit on hosts where their offspring do best (Gripenberg et al., 2010). A good match between the preference of a mated female for a given plant and the performance of their offspring developing on the same plant implies that females can recognize cues that correlate with larval performance, in particular those related to plant defenses and nutritional quality. Yet, these cues can be largely modified by the simultaneous or sequential presence of other competing herbivores (Bultman & Faeth, 1986; Nykänen & Koricheva, 2004; Abdala-Roberts et al., 2019; Visakorpi et al., 2019). Therefore, initial herbivory may have time-lagged consequences of the preference and performance

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of herbivores that subsequently attack the same plant in the same growing season (Poelman et al., 2008; Stam et al., 2014). However, while such time-lagged *interspecific* interactions between herbivores have long been documented (Faeth, 1986), surprisingly much less is known about delayed *intraspecific* interactions in multivoltine species.

Previous herbivory can influence the oviposition preference of later herbivores. Several studies have demonstrated that mated females can discriminate host plants that have been previously attacked by insect herbivores (Wise & Weinberg, 2002; Stam et al., 2014; Moura et al., 2017; Barnes & Murphy, 2018; Moreira et al., 2018; Weeraddana & Evenden, 2019). This behaviour involves the use of a mix of plant and herbivore cues to detect the passage of competitors on potential hosts. Several mechanisms can explain such indirect interactions between herbivores separated in time. First, mated females can directly detect the present, past and possibly future presence of competitors. For instance, Averill & Prokopy (1987) showed that female *Rhagoletis pomonella* Walsh (Diptera: Tephritidae) marks its oviposition site with an epideictic pheromone that deter conspecific females from laying eggs, thus reducing intraspecific competition at the larval stage. The frass of several Lepidoptera species was also found to act as an oviposition deterrent to subsequent herbivores (Jones & Finch, 1987; Hashem et al., 2013; Molnár et al., 2017). Second, herbivory can induce changes in the physical and chemical characteristics of attacked plants (Marchand & McNeil, 2004; Blenn et al., 2012; Fatouros et al., 2012; Hilker & Fatouros, 2015; Abdala-Roberts et al., 2019), thereby reducing their attractivity to mated females.

Previous herbivory generally reduces the performance of later herbivores. A common mechanism is that herbivory induces changes in plant quality and defenses that generally reduce the performance of late coming herbivores (Wratten et al., 1988; Agrawal, 1999; Abdala-Roberts et al., 2019). For instance, prior damage by the western tent caterpillar *Malacosoma californicum* Packard (Lepidoptera: Lasiocampidae) induces the regrowth of tougher leaves acting as physical defenses and reducing the fitness of the next tent caterpillars generation (Barnes & Murphy, 2018). However, several authors reported a mismatch between prior herbivory effects on female oviposition preference *vs* larval growth, consumption or survival of their offspring (Wise & Weinberg, 2002; Bergamini & Almeida-Neto, 2015; Martinez et al., 2017). For instance, Weeraddana and Evenden (2019) found that herbivory by the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) on canola plants (*Brassica napus* L.) had no effect on subsequent oviposition by the bertha armyworm, *Mamestra configurata* Walker (Lepidoptera: Noctuidae) whereas its larvae had reduced growth on previously damaged plants. It follows that a sound understanding of the effect of prior herbivory on subsequent herbivory requires studying its effect on the preference and performance of later herbivores simultaneously.

The box tree moth (BTM) *Cydalima perspectalis* Walker (Lepidoptera: Crambidae) is a multivoltine moth species introduced to Europe in 2007 from Asia (Wan et al., 2014). In its native range, BTM larvae can feed on different host genera, whereas in Europe they feed exclusively on box trees (*Buxus spp*) (Wan et al., 2014). In the introduced area, the BTM overwinters at the larval stage, mainly in the third instar, such that defoliation restarts at the beginning of the growing season. In Europe, damage is aggravated by the fact that the BTM has 3-4 generations a year (Kenis et al., 2013; Matošević et al., 2017). When several pest generations successively defoliate the same box tree, there are no leaves left to eat and the caterpillars then feed on the bark, which can lead to the death of the host tree (Kenis et al., 2013; Wan et al., 2014; Alkan Akıncı & Kurdoğlu, 2019). In the present study, we investigated the consequences of defoliation by the first, spring generation of BTM larvae on the oviposition behaviour of the adults and the larval performance in the next generation. We hypothesized that early herbivory would reduce oviposition on previously attacked hosts and reduce the performance of the next generation larvae feeding on damaged hosts. By addressing the above, our study brings new insights into the understanding of cross-generational intraspecific competition in insect herbivores and further challenges the '*mother knows best hypothesis*'.

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2 Materials and methods

2.1 Biological material

In spring 2019, we obtained box trees from a commercial nursery and kept them in a greenhouse at INRAE Bordeaux forest research station. Box trees were on average 25 cm high and 20 cm wide. We transferred them into 5 L pots with horticultural loam. For two months, we watered them every four days from the above (*i.e.* watering leaves too) to remove any potential pesticide remain.

BTM larvae (L1-L3) overwinter in cocoons tied between two adjacent leaves. We initiated BTM larvae rearing with caterpillars collected in the wild in early spring 2019. We reared them at room temperature in 4320 cm^3 plastic boxes, and fed them *ad libitum*, with branches collected on box trees around the laboratory. At 25°C, the BTM achieves one generation in 45 days. The larval phase lasts for about 30 days. Adults live 12-15 days. A single female lays on average 800 eggs. We initiated the herbivory on box tree plants with larvae which were the offspring of the overwintering generation. Their adults were used in the preference test, and second generation larvae used in the performance test (see below).

2.2 Experimental design

On June 18th 2019, we haphazardly assigned box trees to *control* and *herbivory* experimental groups. The *herbivory* treatment consisted of $n = 60$ box trees that received five L3 larvae each. Larvae were allowed to feed freely for one week, after which we removed them all from plant individuals. In order to confirm that the addition of BTM larvae caused herbivory, we visually estimated BTM herbivory as the percentage of leaves consumed by BTM larvae, looking at every branch on every plant. We then averaged herbivory at the plant level. Herbivory ranged from 2 to 18% and was on average 9%. The *control* group ($n = 61$) did not receive any BTM larva. On July 8th, we randomly distributed plants of the *herbivory* and *control* treatments on a 11×11 grid in a greenhouse. We left 40 cm between adjacent pots, which was enough to avoid any physical contact between neighbouring plants **(Figure 1, Figure 2)**.

Figure 1: Photos illustrating the experimental design.

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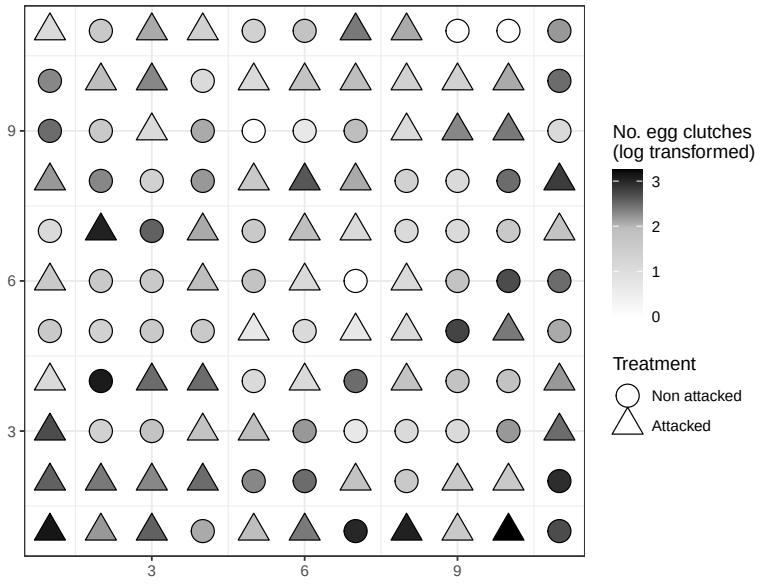

Figure 2: Experimental design. Pots were 40 cm appart. Circles and triangles represent control and non-attacked trees. Scale colour represents the number of egg clutches per box tree (log-transformed).

The same day, we released *ca* 100 BTM moths that had emerged from chrysalids less than two days before (*i.e.*, an uncontrolled mix of males and females). Moths were allowed to fly freely within the greenhouse. They could feedon small pieces of cotton imbibed with a sugar-water solution, disposed on the ground in the greenhouse.

It is important to note that at the time we released moths, there were no larvae feeding on experimental box trees anymore. In addition, at this time, plants in the herbivory treatment had been cleared of caterpillars for three weeks during which they were watered every two to three days from above. Although larval frass may have been present in pots submitted to the herbivory treatment, it should have been washed out. Finally, we carried out our experiment in an enclosed greenhouse in which the potential effect of natural enemies on BTM behaviour can be neglected. The consequences are that any effect of prior herbivory on subsequent oviposition behaviour and larval performance should have been independent of cues emitted by BTM larvae themselves or by their frass (Sato et al., 1999; Molnár et al., 2017) and therefore were only plant-mediated.

2.3 BTM host choice

In order to test whether initial defoliation of focal plants influenced host choice for oviposition by BTM females, we counted egg clutches on every branch of every box tree on July 17th. Once eggs were counted, we moved box trees to another greenhouse. We installed box trees in plastic saucers. We interspaced plants and filled saucers with a few centimeters of water (renewed regularly) to prevent larvae from moving from one potted plant to another.

2.4 BTM growth rate

Fifteen days later (July 31st), we counted larvae on every plant and haphazardly collected five L3 BTM larvae per box tree. We kept them in Petri dishes without food for 24h and weighted them to the closest 10 µg. In some Petri dishes, we observed cases of cannibalism such that in some instances we could only weight two larvae. We therefore calculated the average weight of a L3 larva, dividing the total mass by the number of larvae. Because we did not record the day every single egg hatched, we could not quantify the number of days caterpillars could feed and therefore simply analysed the average weight of a L3 larva.

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Larvae were allowed to complete their development on the potted box trees. After every larvae pupated, we counted the number of chrysalis per box tree and weighted them to the closest 10 µg.

At this stage of the experiment, box trees that had hosted BTM were close to 100% defoliated so that it is possible that some larvae ran out of food before they pupated. In addition, we noticed that the number of chrysalis in 32 control plants (out of 60, *i.e.* 53%) was greater that the number of larvae (and only in 1 previously attacked plant) suggesting that in spite of our precautions some larvae could have moved from attacked to control plots **(Table 1)**. We therefore decided not to analyze data on chrysalis.

2.5 Analyses

All analyses were ran in R using libraries *nlme* and *car* (Fox et al., 2016; Team, 2018; Pinheiro et al., 2020).

We first looked for spatial patterns in female BTM oviposition. We ran a generalized least square model (GLS) testing the effect of x and y coordinates on the number of clutches per plant (*log*-transformed) from which we explored the associated variogram using the functions *gls* and *Variogram* in the *nlme* library. There was evidence that oviposition was spatially structured, with strong spatial autocorrelation between 1 and 3m **(Figure S1)**.

We tested the effect of prior herbivory on female BTM oviposition while controlling for spatial non-independence using a GLS. We had no particular hypothesis regarding the shape of the spatial correlation structure. We therefore ran separate models with different spatial correlation structures (namely, exponential, Gaussian, spherical, linear and rational quadratic), as well as a model with no correlation structure, and compared them based on their AIC (Zuur, 2009). For each model, we computed the ΔAIC (*i.e.*, Δ_i) as the difference between the AIC of each model i and that of the model with the lowest AIC (Burnham & Anderson, 2002). We report and interpret the results of the model with the lowest AIC (see *Results*).

We then tested the effect of prior herbivory on BTM performance using ordinary least square models, with the mean weight of five L3 larvae (*log*-transformed) as a response variable, the herbivory treatment (non-attacked *vs* attacked) as a two-levels factor and the number of egg clutches as a covariate.

3 Results

We counted a total of 818 egg clutches and 593 larvae. At individual box tree level, the number of egg clutches varied from 0 to 25 (mean ± SD: 6.76 ± 5.11, **Figure 2**).

When modelling the effect of prior herbivory on the number of egg clutches, the best model (*i.e.*, model 6 with $\Delta_i = 0$, **Table 2**) was the model with a rational quadratic spatial correlation. It was competing with two other models with $\Delta_i < 2$ **(Table 2)**. The Δ_i of the model with no correlation structure was > 13, confirming that accounting for spatial autocorrelation among plants improved model fit.

Prior herbivory had no significant effect on the number of egg clutches per plant (model 6: $\chi^2 = 2.91$, $P = 0.088$, **Figure 3A**). Competing models 2 and 3 provided the same conclusion.

The weight of BTM larvae varied from 6 to 54 mg (mean ± SD: 20 ± 9 mg). BTM larval weight was lower on box trees that had been previously defoliated (**Table 3**, **Figure 3B**). There was a significant, negative

Table 1: Repartition of egg clutches, larvae and chrysalis across box trees with or without prior herbivory. Numbers correspond to mean (± sd) and total number of egg clutches, larvae or chrysalis (n).

Response variable	Control	Herbivory treatment
Egg clutches	6.1 (4.87), n = 372	7.43 (5.3), n = 446
Larvae	4.84 (0.61), n = 295	4.97 (0.18), n = 298
Chrysalis	6.8 (5.78), n = 415	1.85 (1.79), n = 111

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Table 2: Summary of AIC of GLS models testing the effect of prior herbivory on the number of egg clutches with different spatial correlation structures.

Model	Correlation structure	df	AIC	Delta
Model 1	None	3	262.5	13.1
Model 2	Exponential	5	249.8	0.4
Model 3	Gaussian	5	250.2	0.8
Model 4	Spherical	5	250.9	1.5
Model 5	Linear	5	255.1	5.7
Model 6	Rational quadratic	5	249.4	0.0

relationship between larval weight and the number of egg clutches on a box tree (**Table 3**, **Figure 3B**), suggesting intraspecific competition for food. There was no significant interaction between the herbivory treatment and the number of egg clutches, indicating that intraspecific competition was independent of prior herbivory (**Table 3**). The model explained 29 % variability in larval weight.

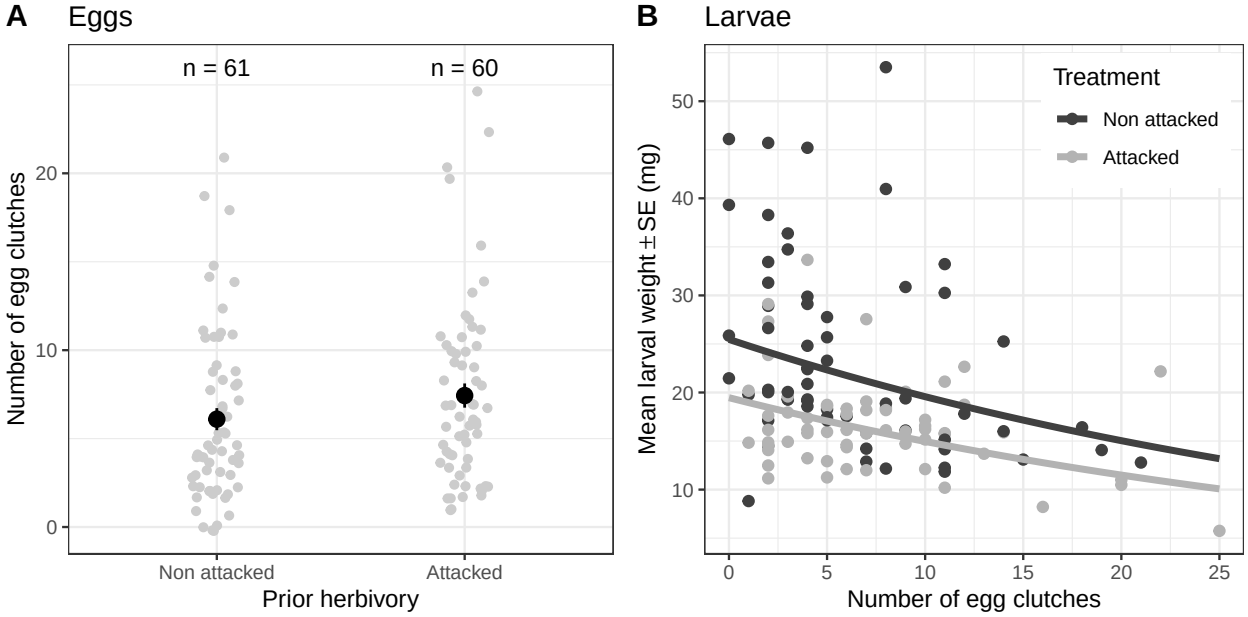

Figure 3: Effects of prior herbivory and conspecific density on (A) the number of egg clutches and (B) L3 larva weight. In A, grey dots represent raw data. Black dots and vertical bars represent raw means (+/- SE). In B, dots represent raw data. Black and grey curves represent model predictions for control and herbivory treatments, respectively.

4 Discussion

Our findings reveal that early season herbivory reduces the performance of conspecific individuals that subsequently attack the same host plant later in the plant growing season, and that this time-lagged intraspecific competition results from a mismatch between female oviposition preference and the performance of its offspring.

Prior herbivory had no effect BTM oviposition choice. Possible explanations are that prior herbivory had no effect on box tree characteristics, or that female BTM were indifferent to them.

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Table 3: Summary of models testing the effect of prior herbivory and initial egg clutch density on BTM larval weight

Predictor	df	Estimate (SE)	F-value	P-value
Number of egg clutches	1, 117	-0.03 (0.01)	20.20	< 0.001
Herbivory	1, 117	-0.34 (0.1)	20.30	< 0.001
Eggs x Herbivory	1, 117	0.01 (0.01)	0.73	0.396

The first explanation seems unlikely as numerous studies have clearly established that insect herbivory induces changes in plant physical and chemical traits, which have profound consequences on herbivores or herbivory on the same host plant latter in the season (Wise & Weinberg, 2002; Poelman et al., 2008; Stam et al., 2014; Abdala-Roberts et al., 2019; but see Visakorpi et al., 2019). For instance, Barnes and Murphy (2018) recently observed that the number of eggs laid by western tent caterpillar (*Malacosoma californicum*) females was much lower on chokecherry trees (*Prunus virginiana*) that have been defoliated by conspecific caterpillars earlier in the season, as a likely result of induced increase in leaf toughness. In our case, it is also possible that induced defense reactions were delayed in box trees, or that they were already relaxed when we released BTM moths three weeks after the herbivory treatment (Karban, 2011), which remains to be evaluated.

We cannot dismiss the second explanation that BTM females were indifferent to box tree cues related to earlier herbivory. This may be particuarly true in species whose females individually lay several hundred eggs, thus corresponding to a within-generation bet-hedging strategy (Root & Kareiva, 1984; Hopper, 1999). Consistently, Leuthardt and Baur (2013) observed that BTM females evenly distributed egg clutches among leaves and branches, and that oviposition preference was not dictated by the size of the leaves. Assuming that this behavior is reproducible, the close distance between box-trees that we used in the present experiment (40 cm) could explain the lack of effect of initial defoliation on BTM oviposition behavior. In addition, Leuthard *et al.* (2013) showed that BTM larvae are able to store or metabolise highly toxic alkaloid present in box tree leaves. Last, BTM larvae proved to be unable to distinguish between box tree leaves infected or not by the box rust *Puccinia buxi*, while their growth is reduced in the presence of the pathogenic fungus (Baur et al., 2019). Altogether, these results suggest that BTM female moths are not influenced by the amount of intact leaves and probably not either by their chemical quality when choosing the host plant, perhaps because of their strong ability to develop on toxic plants.

Prior box tree defoliation by the spring generation of BTM larvae reduced the growth of the next generation. Two alternative, non-mutually exclusive mechanisms can explain this pattern. First, the reduced performance of individuals of the second generation can have been trait-mediated and have resulted from induced plant defenses. This explanation is in line with studies that have documented in several plant species reduced herbivore performance and changes in plant-associated herbivore communities linked to induced defenses after prior herbivory (Nykänen & Koricheva, 2004; Karban, 2011; Stam et al., 2014). In the case of multivoltine species, negative relationship between prior herbivory and subsequent larva growth rate would indicate intraspecific plant-mediated cross-generation competition between cohorts of herbivores separated in time (Barnes & Murphy, 2018), which could influence herbivore population dynamics and distribution across host individuals. However, this explanation is partially conflicting with previous observations that BTM larva growth rate did not differ significantly among box-tree varieties, suggesting broad tolerance to variability in host traits (Leuthardt et al., 2013). Alternatively, reduced performance on previously defoliated plants may partly result from food shortage and increased exploitative competition among larvae of the same cohort. Although free living mandibulate herbivores were described to be less sensitive to competition (Denno et al., 1995), the effect of food shortage may have been exacerbated by the small size of box trees and interference competition, for instance through cannibalism (Kaygin & Taşdeler, 2019) (Schillé and Kadiri, *personal observation*).

Herbivore feeding behavior is an important determinant of herbivore adaptive response to plant defenses (Karban, 2011; Weeraddana & Evenden, 2019). Yet, in our case, larvae were not allowed to move freely and leave the potted tree to find a more suitable host, or more generally escape competition. It is therefore possible that our experimental setup overestimates the effect of intraspecific competition. Whether this

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finding is relevant to real world interactions remains to be tested.

We detected a negative relationship between the number of egg clutches laid by BTM female moths and the subsequent growth of BTM larvae. This suggests the existence of intraspecific competition for food with the same cohort. Such competition has already been reported, particularly in leaf-miners (Bultman & Faeth, 1986; Faeth, 1992), which are endophagous insect herbivores whose inability to move across leaves makes them particularly sensitive to the choice of oviposition sites by gravid female. In our study, we prevented larvae from moving from one plant to another and noticed that some box trees were completely defoliated by the end of the experiment. Although we did not record this information, it is very likely that larvae first ran out of food in plants on which several egg clutches were laid. We are however unable to determine whether the observed intraspecific competition in this cohort was determined by food shortage, or by herbivore-induced changes in resource quality, or both.

5 Conclusion

Our greenhouse experiment provides evidence for negative interaction across and within BTM generation, which are independent of BTM female choice for oviposition site. Such interactions may have consequences on BTM population dynamics and damage on box-trees. On the one hand, the slow-growth-high-mortality hypothesis states that any plant trait reducing the growth rate of herbivores can be seen as a resistance trait, because slow-growing herbivores are longer exposed to their enemies (Benrey & Denno, 1997; Coley et al., 2006; Uesugi, 2015). It is therefore possible that a stronger top-down control can be exerted by generalist enemies on BTM larvae feeding on previously defoliated hosts which could reduce damage on box-trees. On the other hand, if herbivores take a longer time to complete development, they may be more damaging to plants, in particular to plants with low nutritional quality as a result of compensatory feeding (Simpson & Simpson, 1990; Milanovic et al., 2014). The consequences of time-lagged intraspecific competition on the spread of and damage by BTM remain however to beinvestigated in the field. Particular efforts should be dedictaed to the identification of host traits controlling the performance of BTM larvae and the the interaction between these traits and the the higher trophic level.

6 Acknowledgements

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7 Data accessibility

Raw data as well as codes of statistic analysis are available in supplementary material and on the INRA dataverse: Castagneyrol, Bastien; van Halder, Inge; Kadiri, Yasmine; Schillé, Laura; Jactel, Hervé, 2020, "Raw data for the paper 'Host-mediated, cross-generational intraspecific competition in a multivoltine herbivore species', https://doi.org/10.15454/KMUX39, Portail Data INRAE, V1

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9 Appendix

9.1 Supplementary figure

Figure S1 - Semivariogram of the number of egg clutches as a function of distance among box trees.

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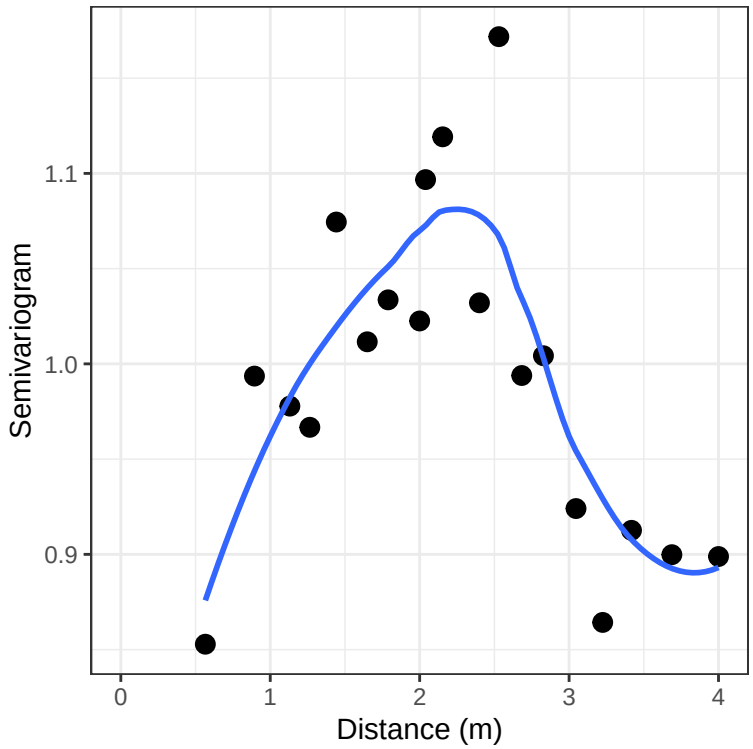

9.2 Supplementary table containing raw data

Table S1 - Raw data used in the present manuscript: `x` and `y` are the position of each box tree in the green house; `Treatment` is the prior herbivory treatment; `Clutch.number` is the total number of egg clutches counted on a given box tree; `N.L3` is the number of retrieved L3 larvae, `L3.mean` is the mean weight of a L3 larvae (g); `N.chrysalids` is the number of retroved chrysalids; `Chrysalid.mean` is the mean weight of a chrysalid.

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x	y	Treatment	Clutch.number	N.L3	L3.mean	N.chrysalids	Chrysalid.mean
1	1	Attacked	22	5	0.0221740	0	NaN
2	1	Attacked	8	5	0.0183980	0	NaN
3	1	Attacked	12	5	0.0187360	1	0.1020100
4	1	Non attacked	7	5	0.0142200	6	0.1612240
5	1	Attacked	6	5	0.0146140	0	NaN
6	1	Attacked	10	5	0.0165620	2	0.1101750
7	1	Non attacked	19	5	0.0140740	6	0.1295600
8	1	Attacked	20	5	0.0110140	1	0.0961900
9	1	Attacked	4	5	0.0132300	1	0.1438500
10	1	Attacked	25	5	0.0057520	1	0.0891900
11	1	Non attacked	14	5	0.0252560	4	0.0800775
1	2	Attacked	12	5	0.0226500	2	0.2062350
2	2	Attacked	10	5	0.0162200	1	0.0524100
3	2	Attacked	9	5	0.0200760	0	NaN
4	2	Attacked	11	5	0.0211200	5	0.1465000
5	2	Non attacked	9	5	0.0160880	2	0.1455000
6	2	Non attacked	11	4	0.0332225	11	0.1486660
7	2	Attacked	5	5	0.0112560	0	NaN
8	2	Non attacked	4	5	0.0192900	10	0.1718880
9	2	Attacked	4	5	0.0161760	1	0.1338800
10	2	Attacked	4	5	0.0173680	1	0.1706800
11	2	Non attacked	18	5	0.0164180	1	0.1142100
1	3	Attacked	14	5	0.0159000	4	0.1686525
2	3	Non attacked	3	5	0.0193180	8	0.1842200
3	3	Non attacked	5	5	0.0277660	10	0.1413480
4	3	Attacked	5	5	0.0159420	2	0.1380100
5	3	Attacked	6	5	0.0121100	1	0.1319100
6	3	Non attacked	8	5	0.0535020	9	0.1464700
7	3	Non attacked	1	5	0.0197740	11	0.1815320
8	3	Non attacked	2	5	0.0334440	9	0.2104500
9	3	Non attacked	2	5	0.0144920	2	0.1980650
10	3	Non attacked	8	5	0.0188620	7	0.1529100
11	3	Attacked	11	5	0.0101960	1	0.0836300
1	4	Attacked	2	5	0.0111600	2	0.1224050
2	4	Non attacked	21	5	0.0127880	2	0.1022250
3	4	Attacked	11	5	0.0157420	0	NaN
4	4	Attacked	11	5	0.0158140	4	0.1557575
5	4	Non attacked	2	5	0.0171240	1	0.1575800
6	4	Attacked	2	5	0.0238660	2	0.1728600
7	4	Non attacked	11	5	0.0151460	0	NaN
8	4	Attacked	5	5	0.0187260	2	0.1527050
9	4	Non attacked	5	5	0.0256880	5	0.1158560
10	4	Non attacked	5	5	0.0171440	3	0.1927033
11	4	Attacked	8	5	0.0181900	0	NaN
1	5	Non attacked	4	5	0.0185720	3	0.1905400
2	5	Non attacked	3	5	0.0363840	20	0.1862420
3	5	Non attacked	4	5	0.0224060	8	0.1504320
4	5	Non attacked	4	5	0.0291180	9	0.1339320
5	5	Attacked	1	5	0.0201820	1	0.1914500
6	5	Non attacked	2	5	0.0313100	2	0.1725900
7	5	Attacked	1	5	0.0148320	3	0.1752800
8	5	Attacked	2	5	0.0176160	1	0.0853400
9	5	Non attacked	15	5	0.0130960	1	0.1001600
10	5	Attacked	10	4	0.0171925	1	0.1453700
11	5	Non attacked	7	5	0.0128840	2	0.1279200
1	6	Attacked	4	5	0.0158160	2	0.1774000
2	6	Non attacked	4	5	0.0225620	11	0.1544600

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9.3 All code for this report

```
library(tidyverse)
library(knitr)
library(kableExtra)
library(nlme)
library(car)
library(citr)
library(here)

wd = here()

my.ggplot <- function(){
  theme_bw() +  theme(legend.key = element_blank())
}

knitr::opts_chunk$set(echo= F, warning= F, message = F, results = "hide",
                      fig.width=4, fig.height=4, dpi= 100, fig.pos = "H",
                      fig.path = paste0(wd, '/Figures/'))

d = read.csv(paste0(wd, '/Data/BTM_data.csv'), header = T)

str(d)

d =
  d %>% mutate(L3.mean = Weight.L3 / N.L3) %>%
  mutate(Treatment = factor(Treatment, levels = c("Non attacked", "Attacked")))
knitr::include_graphics(paste0(wd, '/Figures/Figure 1.png'))

d %>%
  ggplot(aes(x, y, shape = Treatment, fill = log1p(Clutch.number))) +
  # geom_rect(aes(xmin = 1.5, ymin = 1.5, xmax = 10.5, ymax = 10.5), fill = 'grey90') +
  geom_point(size = 6) +
  scale_shape_manual(values = c(21, 24)) +
  my.ggplot() +
  labs(x = "", y = "") +
  scale_fill_gradientn(colours = c('white', 'grey', 'black'), values = c(0,0.6,1), name = 'No. egg clut
d %>%
  select(Treatment, Clutch.number, N.L3, N.chysalids) %>%
  gather(Resp, Val, 2:4) %>%
  group_by(Treatment, Resp) %>%
  summarise(N = sum(Val), M = round(mean(Val),2), SD = round(sd(Val),2)) %>%
  mutate(Val = paste(M, ' (', SD, ')', ', n = ', N, sep = '')) %>%
  select(- N, - M, - SD) %>%
  mutate(Resp = factor(Resp, levels = c('Clutch.number', 'N.L3', 'N.chysalids'), labels = c('Egg clutch
  spread(Treatment, Val) %>%
  kable(col.names = c('Response variable', 'Control', 'Herbivory treatment'),
        caption = "Repartition of egg clutches, larvae and chrysalis across box trees with or without p
d.center = droplevels(d[d$x > 1 & d$x < 11 & d$y > 1 & d$y < 11,])
m0 = gls(log1p(Clutch.number) ~ Treatment, data = d, na.action = "na.omit")
m1a = gls(log1p(Clutch.number) ~ Treatment, correlation = corExp(form = ~x + y, nugget = TRUE), data = 
m1b = gls(log1p(Clutch.number) ~ Treatment, correlation = corGaus(form = ~x + y, nugget = TRUE), data =
m1c = gls(log1p(Clutch.number) ~ Treatment, correlation = corSpher(form = ~x + y, nugget = TRUE), data =
```

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```
m1d = gls(log1p(Clutch.number) ~ Treatment, correlation = corLin(form = ~x + y, nugget = TRUE), data = d
m1e = gls(log1p(Clutch.number) ~ Treatment, correlation = corRatio(form = ~x + y, nugget = TRUE), data =

Table_AIC = AIC(m0, m1a, m1b, m1c, m1d, m1e)
Table_AIC$AIC = round(Table_AIC$AIC,1)
Table_AIC$Delta = Table_AIC$AIC - min(Table_AIC$AIC)
# Table_AIC %>% kable() %>% kableExtra::kable_styling()

# plot_resid = function(model) {
#   df = data.frame(Residuals = residuals(model),
#                   Fitted = fitted(model))
#
#   A = df %>% ggplot(aes(Fitted, Residuals)) +
#     my.ggplot() +
#     geom_point() +
#     geom_smooth(method = "lm", se = F) +
#     geom_hline(yintercept = 0)
#
#   B = df %>% ggplot(aes(Residuals)) + my.ggplot() + geom_histogram()
#
#   cowplot::plot_grid(A, B)
# }
#
# plot_resid(m1e)
# Alternative approach fitting *x* and y*y position in the greenhouse together with`treatment` and `N.a
#
# m = MASS::glm.nb(Clutch.number ~Treatment * N.attacked, data = d.center)
# Anova(m)
# #
# # var.resid = Variogram(residuals(m), dist(d.center %>% select(x, y)))
# # var.resid %>%
# #   ggplot(aes(dist, variog)) +
# #   my.ggplot() +
# #   # geom_point(size = 3) +
# #   geom_smooth(se = F) +
# #   labs(x = "Distance (m)", y = "Semivariogram")
plot.resid = function(m){
  df = data.frame(f = fitted(m), r = residuals(m))
  A = df %>%
    ggplot(aes(f, r)) + my.ggplot() + geom_point() + geom_smooth(method = "lm", se = F) + geom_hline(yi
  B = df %>%
    ggplot(aes(r)) + my.ggplot() + geom_histogram()
  cowplot::plot_grid(A,B)
}

m_larvae = lm(log(L3.mean) ~ Clutch.number * Treatment , d)

# plot.resid(m_larvae)

d =
  d %>%
  mutate(Chrysalid.mean = Weight.chrysalids / N.weighted.chysalids)
```

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```
m_chrys = lm(log(Chrysalid.mean) ~ Clutch.number * Treatment , d)
# plot.resid(m2)
Table_AIC %>%
  mutate(Model = paste('Model', 1:6),
         'Correlation structure' = c('None', 'Exponential', 'Gaussian', 'Spherical', 'Linear', 'Rational
  select(Model, `Correlation structure`, everything()) %>%
  kable(caption = "Summary of AIC of GLS models testing the effect of prior herbivory on the number of e
Anova(m1e)

Fig_3A =
  d %>%
  ggplot(aes(Treatment, Clutch.number)) +
  my.ggplot() +
  geom_point(position = position_jitter(0.1), colour = "grey80") +
  stat_summary(size = 0.6) +
  labs(x = "Prior herbivory", y = "Number of egg clutches") +
  annotate(geom = 'text', x = 1:2, y = 26, label = paste("n =", c(61, 60)))
res_larvae = Anova(m_larvae)
n = expand.grid(Treatment = levels(d$Treatment), Clutch.number = seq(0, 25))
p = predict(update(m_larvae, ~.- Clutch.number:Treatment), newdata = n)
n$Fit = 1000 * exp(p)

Fig_3B =
  d %>%
  ggplot(aes(Clutch.number, 1000 * L3.mean, colour = Treatment)) +
  my.ggplot() +
  geom_point(size = 2) +
  scale_colour_manual(values = c("grey25", "grey70")) +
  labs(x = "Number of egg clutches",
       y = expression("Mean larval weight" %+-% "SE (mg)")) +
  geom_line(data = n, aes(Clutch.number, Fit), size = 1.5) +
  theme(legend.position = c(0.8, 0.85))
r = with(d, cor.test(Chrysalid.mean, L3.mean))

cowplot::plot_grid(
  Fig_3A + labs(title = 'Eggs'),
  Fig_3B + labs(title = 'Larvae'),
  ncol = 2,
  labels = c('A', 'B')
)
X = c("Number of egg clutches", "Herbivory", "Eggs x Herbivory")
Fval = function(x) {round(x[,3], 2)}
Pval = function(x) {ifelse(x[,4] < 0.001, '< 0.001', round(x[,4], 3))}
df = rep("1, 117", 3)
b = round(summary(m_larvae)$coefficients[-1,1], 2)
b_se = round(summary(m_larvae)$coefficients[-1,2], 2)
Estimate = paste(b, ' (', b_se, ')', sep = '')

data.frame(#Response = c('Larvae', '', ''),
           Predictor = X,
           df = df,
           Estimate = Estimate,
           `F-value` = Fval(res_larvae)[-4],
```

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```
            `P-value` = Pval(res_larvae)[-4]) %>%
  kable(caption = "Summary of models testing the effect of prior herbivory and initial egg clutch densi
        col.names = c("Predictor", "df", "Estimate (SE)", "F-value", "P-value"),escape = T, digit = 2) %
m0 = gls(log1p(Clutch.number) ~ x + y, data = d, na.action = "na.omit")
variog0 <- Variogram(m0, form = ~x + y, resType = "pearson", nugget = T)
variog0 %>%
  ggplot(aes(0.4*dist, variog)) +
  my.ggplot() +
  geom_point(size = 3) +
  geom_smooth(se = F) +
  labs(x = "Distance (m)", y = "Semivariogram") +
  xlim(0, 4)
d %>%
  rename(N.chrysalids = N.chysalids) %>%
  select(x, y, Treatment, Clutch.number, N.L3, L3.mean, N.chrysalids, Chrysalid.mean) %>% kable() %>% ka
```