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Order of herbivore arrival on wild cabbage populations influences subsequent arthropod community development

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In plant–arthropod associations, the first herbivores to colonise a plant may directly or indirectly affect community assembly on that particular plant. Whether the order of arrival of different arthropod species further modulates community assembly and affects plant fitness remains unclear.

Using wild *Brassica oleracea* plants in the field, we manipulated the order of arrival of early-season herbivores that belong to different feeding guilds, namely the aphid *Brevicoryne brassicae* and caterpillars of *Plutella xylostella*. We investigated the effect of herbivore identity and order of arrival on community assembly on two *B. oleracea* plant populations during two growth seasons. For this perennial plant, we evaluated whether foliar herbivory also affected herbivore communities on the flowers and if these interactions affected plant seed production.

Aphid infestation caused an increase in parasitoid abundance, but caterpillars modulated these effects, depending on the order of herbivore infestation and plant population. In the second growth season, when plants flowered, the order of infestation of leaves with aphids and caterpillars more strongly affected abundance of herbivores feeding on the flowers than those feeding on leaves. Infestation with caterpillars followed by aphids caused an increase in flower-feeding herbivores compared to the reversed order of infestation in one plant population, whereas the opposite effects were observed for the other plant population. The impact on plant seed set in the first reproductive year was limited.

Our work shows that the identity and arrival order of early season herbivores may have long-term consequences for community composition on individual plants and that these patterns may vary among plant populations. We discuss how these community processes may affect plant fitness and speculate on the implications for evolution of plant defences.

Keywords: *Brassica oleracea*, community dynamics, historical contingency, priority effects, herbivory, induced response, plant-mediated insect interactions, plant population

Introduction

The historical contingency of how the presence of individual species affects community assembly is an important determinant of community structure in many terrestrial and aquatic ecosystems (Chase 2003, Trussell et al. 2003, Křivan and Schmitz 2004, Schmitz et al. 2004, Fukami 2015). Historical contingency may result from direct species interactions such as density dependent effects in trophic relationships, or from indirect species interactions (Werner and Peacor 2003). These indirect interactions frequently result from one organism altering the quality of a resource that it shares with other community members (Werner and Peacor 2003). Consequently, this organism may initiate horizontal interactions with other species at the same trophic level as well as extending its effect to species from vastly different functional groups that have no trophic relationship, such as elephants and lizards, herbivores and pollinators or bivalves and barnacles (Paine 1966, Ohgushi 2005, Kessler and Halitschke 2007, Pringle 2008). How species affect one another depends on priority effects determined by the order and timing of species joining the community (Chase 2003). In complex food webs it is therefore crucial to consider historical contingency to understand community structure as well as the evolutionary regime under which selection on community members occurs (Urban and De Meester 2009, Fukami 2015).

In arthropod–plant interactions, historical contingency consists of intricate interaction networks that are particularly important for community dynamics on individual plants (Utsumi et al. 2010). In these networks, the first arriving herbivore species may affect the likelihood of plant colonization by and performance of a subsequent herbivore (Agrawal 2000, Poelman et al. 2008). Moreover, herbivore species have been found to have differential season-long effects on the colonisation of the plant by other herbivores as well as their predators and parasitoids (van Zandt and Agrawal 2004, Viswanathan et al. 2005, Poelman et al. 2010, Stam et al. 2014, Li et al. 2016). The historical contingency on community assembly has both bottom–up and top–down components that are frequently heavily entwined (Utsumi et al. 2010, Kos et al. 2011, Leopold et al. 2017). For example, individual herbivores may promote abundance of associated predators and parasitoids that in turn may have top–down effects on this as well as other herbivore species (Utsumi et al. 2010, Kos et al. 2011).

Leaf-feeding herbivores have also been found to affect flower visitation by pollinators as well as herbivory on reproductive tissues (McArt et al. 2013, Rusman et al. 2018). Species in this group of flower-associated community members can also differ in their responses to leaf-feeding herbivores (Rusman et al. 2018). The responses of the flower-associated community to leaf herbivory may lead to effects on seed number or quality and thus affect plant reproductive success (McArt et al. 2013, Rusman et al. 2018). Although priority effects have been identified as of major importance in arthropod–plant community organisation (Stam et al.

2014), and even in natural selection on plant defence strategies (Lankau and Strauss 2008, Poelman and Kessler 2016), several questions remain. A major knowledge gap is whether and how priority effects in the order and timing of arrival of multiple herbivore species may modulate the assembly of the arthropod community on individual plants. There is particularly limited understanding of whether priority effects in the arrival of multiple herbivores affects plant fitness (McArt et al. 2013, Poelman 2015, Rusman et al. 2018).

Here, we studied the priority effects of early-season feeding by two herbivores from different feeding guilds, and the order of their arrival, on arthropod community assembly on perennial wild *Brassica oleracea* plants. This was done for plants from two different populations (Kimmeridge (KIM) and Winspit (WIN)) over a total period of two years. Our study focussed on three major outstanding questions on priority effects of plant–arthropod community assembly: 1) Does the identity of early-season herbivores, either phloem-feeding aphids or leaf-chewing caterpillars, affect season-long arthropod community assembly? 2) Does the order of arrival of these two herbivores affect arthropod community assembly? And 3) are priority effects by leaf feeding herbivores affecting floral associated communities with effects on plant seed production? We predicted that because of their different feeding styles and associated predators, aphids and caterpillars would affect assembly of the community differently (Bidart-Bouzat and Kliebenstein 2011, Vos et al. 2013). Moreover the order of arrival of aphids and caterpillars likely modulates community assembly, because plant responses to single and dual herbivory are highly specific resulting in unique plant phenotypes that potentially affect interactions with herbivores, predators and flower visitors (Viswanathan et al. 2007, Erb et al. 2011, Miller-Pierce and Preisser 2012, Soler et al. 2012, Ali and Agrawal 2014, Lucas-Barbosa et al. 2014). We analysed priority effects in early-season herbivore arrival on plant seed production, and predicted that order of arrival affects this plant fitness proxy based on earlier findings that leaf herbivory affects seed predation (McArt et al. 2013) as well as pollinator visitation (Lucas-Barbosa et al. 2014, Rusman et al. 2018). We discuss how priority effects in dynamic arthropod–plant community processes may have implications for evolution of induced plant defences.

Material and methods

Plants and insects

In a common-garden experiment, wild perennial *Brassica oleracea* (Brassicaceae) plants from two plant populations were used. Seeds had been collected from *B. oleracea* populations on the southwestern coast of England, at Winspit (50°35′N, 2°02′W) and Kimmeridge (50°36′N, 2°07′W) (Gols et al. 2008). These plant populations were chosen for their known differences in induced secondary compounds and responses to insect herbivory (Gols et al. 2008, Newton et al. 2009,

Li et al. 2014, 2016). Seeds were sown directly onto peat soil and 11-day-old seedlings were transplanted into peat soil cubes. One week prior to planting, seedlings were placed outside (under a roof shelter) to condition them to field conditions. In week 21 (mid-May) 2012, five-week-old plants were planted directly into the soil of the field site. During the field seasons, plots were manually weeded at regular time intervals and grass strips between plots were regularly mown.

After the 2012 field season, the perennial *B. oleracea* plants remained in the field site during winter, and were used next spring for the 2013 field season. The plants were covered with cloth (26 g m^{-2}) from 8 January 2013 until 3 April 2013 to avoid dehydration of the plants by frost during the coldest part of the winter.

Cabbage aphids, *Brevicoryne brassicae* (Hemiptera: Aphididae), and diamondback moth caterpillars, *Plutella xylostella* (Lepidoptera: Yponomeutidae), were used as herbivores to induce the plants early in the season. Both species are specialists on Brassicaceae, occur on the natural cabbage populations used in our study (Moyes et al. 2000) and colonize plants early in the season, although not necessarily in a fixed order (Poelman et al. 2009, 2010). The insects originated from cultures maintained at the Laboratory of Entomology, Wageningen Univ., the Netherlands, and were reared on Brussels sprout plants (*B. oleracea* var. *gemmifera* cv. Cyrus) under standardized conditions (21 ± 1°C, 50–70 % relative humidity, 16L : 8D cycle) in a climate chamber.

Common garden design

We established 96 plots in a field site in the vicinity of Wageningen Univ., each with a monoculture of 12 plants in a 4 × 4 square (omitting the four central plants to ensure equal plant neighbouring effects for all plants per plot). Each plot was planted with plants from either of the two plant populations, with a between-plant distance of 1 m and 4 m wide strips sown with a *Poa/Lolium* mixture directly after planting to separate the plots. Native *Brassica nigra* (Brassicaceae) plants, grown and planted similarly to the method described for the *B. oleracea* plants, were used as an edge (a strip of 1 m wide with two rows of plants, 0.5 m distance within-row, at 4 m distance from the plots) surrounding the experimental field, to homogenize edge effects. In week 21 of the second year (2013), new *B. nigra* seedlings were planted.

In all herbivore treatments during both years, *B. brassicae* aphids were 4th instar nymphs to adults and *P. xylostella* caterpillars were in the second larval stage (L2). In week 22 (29 May) of 2012, we subjected the 96 plots (half of which were KIM and half WIN plants) to the following six herbivore treatments: no herbivores (none); five *B. brassicae* aphids (A); three *P. xylostella* caterpillars (C); five *B. brassicae* aphids and three *P. xylostella* caterpillars simultaneously (A&C); five *B. brassicae* aphids, followed six days later by three *P. xylostella* caterpillars (A–C); or three *P. xylostella* caterpillars, followed six days later by five *B. brassicae* aphids (C–A). All 12 *B. oleracea* plants in the plot received the same herbivore treatment. The number of herbivores were chosen to

resemble natural early-season colonisation; the time interval of six days between addition of the two herbivores was used to allow full deployment of plant responses to the first herbivore (Poelman et al. 2008, 2010), and insects were not removed to mimic the natural colonisation process. For each population, each treatment had eight replicates (plots), which were completely randomized over the 1-ha field site.

In the second year, we focussed only on the effects of order of early herbivore arrival, due to the labour intensive monitoring of two year old fully grown flowering plants. Although all plants received the same herbivore treatment in the two years, we focused our analyses in the second year on the plants that had received a dual-induction treatment (A&C, A–C, C–A). Inoculation of herbivores was done in week 20 (16 May 2013) for the first herbivore and six days later in week 21 (22 May 2013) for the second.

Monitoring arthropod community

One week after the first round of herbivore infestation in 2012, four plants per plot were chosen that clearly showed feeding by the herbivores (typical *P. xylostella* feeding damage and caterpillar or aphid presence), indicating that herbivores had established. These four plants were monitored throughout the season at 12 time points (weeks 23–41), each time point taking 1–2 weeks and at every time point the same four plants were monitored (excluding the few plants that died during the season). Because the perennial *B. oleracea* plants were larger in 2013 and flowered in that year, monitoring of the arthropod community was more time consuming than in the previous year and thus done at only two time points: early in the season (round 1, week 21–25) and in mid-season (round 2, week 25–33). During monitoring, each leaf was carefully checked on both sides for all occurring insects and other organisms (e.g. including spiders, snails); excluding fast-flying insects such as butterflies and parasitoids as they could not accurately be assigned to individual plants. All visible life stages (egg, larva, pupa, adult except when fast flying) were recorded and summed per species. In 2013, for each insect found we recorded whether it occurred on the vegetative (leaves) or reproductive (flowers and flower stems) part of the plant, which we refer to as the leaf- and flower-associated communities, respectively. Although pollinators are the predominant part of the flower-associated community, we omitted pollinators because as fast flying insects they could not be accurately be assigned to individual plants (see Supplementary material Appendix 1 Table A1 for list of recorded arthropods).

Harvesting seeds

To determine whether the order of early-season arrival by the two herbivores affected seed production (as a proxy of plant fitness) in the first season of reproduction, all seeds of the monitored *B. oleracea* plants that received both early herbivore species (A&C, A–C, C–A) were harvested after the last round of monitoring. Flower stalks with dried seed pods were cut and placed in a paper bag for each plant; a cloth

underneath the plant was used to collect all seeds that fell during the procedure. Bag contents were processed after storage to separate seeds from seed pods and other plant material. The numbers of obtained seeds were estimated by weighing 100 seeds per plant and weighing the total plant seed harvest, computing total seed number per plant by dividing total mass by average seed weight.

Statistical analysis

We first explored whether herbivore induction treatments as well as plant population had effects on quantitative aspects of the insect community. As quantitative measures, we assessed insect abundance and species richness per plot in both years. For abundance, numbers of insects per plot were transformed ($x = x_i/x_{max}$) to rescale to values between 0 and 1, because abundances differed by a factor 10–1000 between species (Zuur et al. 2007), and total insect abundance in a plot was averaged over the whole season. Species richness was represented by the total number of insect species recorded per plot over the whole season. The measurements for abundance and species richness were found to be approximately normally distributed and have equal variances. Effects of early-season herbivory treatment, plant population and their interaction on total herbivore and carnivore abundance and richness in both years were therefore analysed by two-way ANOVA.

Due to our research questions on community development after early-season herbivory having a time component and also addressing the qualitative aspect of community composition, we used time series multivariate ordination techniques. In all these analyses, arthropod numbers per species were summed for all monitored plants in a plot, divided by the number of plants monitored in that plot and log (n + 0.25) transformed for analyses. *Brevicoryne brassicae* and *P. xylostella* were excluded from the analyses, because their numbers were directly manipulated during experiments (Supplementary material Appendix 1). To post hoc compare (pairwise) effects of treatments and/or plant populations on the whole arthropod community, on functional groups (herbivores, predators, parasitoids) or plant parts (vegetative or reproductive), we selected subsets of plots, or species for analyses. Plant population × early season herbivore treatment interactions were analysed using treatments defined as the plant population–herbivore treatment combination (e.g. WIN A&C). All ordination analyses were executed with Canoco 5.04 for Windows (ter Braak and Šmilauer 2012).

We addressed our three research questions of 1) effects of early-season herbivore identity (aphid or caterpillar), 2) effects of dual herbivory and their order of arrival, 3) specificity of these effects for leaf and flower communities, using the ordination technique principal response curves (PRC; Šmilauer and Lepš 2014). For each comparison, separate redundancy analyses (RDAs) with monitoring time points as covariate were performed using a Monte Carlo permutation test (499 permutations, with hierarchical design for the randomized plots × time points). Resulting PRC plots show relative differences in community composition on the first ordination axis over time, along with a species score plot which indicates the relative species abundance in the community, as affected by the treatments tested. See supplementary material Appendix 1 for interpretation of the resulting PRC graphs. Using the insect community data of 2012, for which the community was sampled 12 times throughout the season, we constructed PRC plots for each of the two plant populations, testing the relative difference in community composition for each of the five herbivore treatments to the baseline community of the plants that did not receive early-season herbivory (none). To further elaborate on the second research question on the order and time interval between infestation with the two herbivore species, we compared the treatments C–A, A–C and C&A for the two time points of insect community composition in 2013. We used RDA, a linear constrained ordination technique, which was suitable for our arthropod data that had a gradient of less than 3 turnover (SD) units long (Šmilauer and Lepš 2014). To take into account that each of the two monitoring rounds took several weeks to complete, week number was used as a covariate in the analyses (i.e. partial RDA). Partial RDAs were performed using a Monte Carlo permutation test (499 unrestricted permutations). Resulting RDA plots show species (arrows) and treatment (square centroids) ordination, with (large) arrows and centroids pointing in the same direction having a high correlation. See supplementary material Appendix 1 for interpretation of the resulting RDA biplots.

The number of seeds from plants treated with different orders of early herbivore arrival (A&C, A–C, C–A), the two plant populations (Winspit and Kimmeridge), and their interaction term were analysed by ANOVA. The number of seeds from individually monitored plants was double square root transformed prior to analysis to meet assumptions of normality and homogeneity. ANOVAs for cumulative *B. brassicae* numbers, insect abundance and species richness, and seed numbers were performed with SPSS ver. 19.0.0.1.

Data deposition

Arthropod abundance and species richness data, community composition data and seed set data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.f41b11f> (Stam et al. 2018).

Results

Arthropod community

Insect abundance and species richness
In the first year (2012) both herbivore and carnivore abundance were affected by plant population, with a higher abundance on Winspit plants. Neither early-season herbivory treatments nor the interaction with plant population affected abundance or species richness in either year (Supplementary material Appendix 1 Table A2).

Effect of identity of early-season herbivores and its specificity per plant population

By using ordination analyses that provide much more detailed analyses of the community dynamics through time than species abundance or richness, we identified that early-season herbivory in the first year (2012) had an effect on arthropod community composition during the remainder of the season for both Winspit and Kimmeridge plants (PRC, Winspit plants: first axis explained 5.86%, Monte Carlo permutation test, pseudo-$F_{60,11}$: 31.4; p = 0.002, Fig. 1a; and on Kimmeridge plants: first axis explained 4.46%, Monte Carlo permutation test, pseudo-$F_{60,11}$: 23.5; p = 0.002; Fig. 1b). Moreover, plant populations differed in the effects of early herbivory on the arthropod community throughout the season (PRC, first axis explained 1.37%, Monte Carlo permutation test, pseudo-$F_{12,11}$: 15.7, p = 0.002), and the effects of plant population and early-season herbivore infestation showed a significant interaction (PRC, first axis explained 5.48%, Monte Carlo permutation test, pseudo-$F_{60,11}$: 29.2, p = 0.002). Therefore, the plant populations were analysed separately for the remainder of this study.

When comparing the effect of the identity of single early-season herbivores, aphids (A) placed on Winspit plants early in the season affected season-long development of the plant-associated insect community differently to plants that had an early-season caterpillar treatment (C), or plants without early-season herbivore infestation (noneone) (Supplementary material Appendix 1 Table A3, Fig. 1a). In contrast, on Kimmeridge plants early-season herbivory by aphids or caterpillars did not significantly affect the insect community (Supplementary material Appendix 1 Table A3, Fig. 1b).

When the responding arthropod community was divided into different functional groups (herbivores, predators, parasitoids, Supplementary material Appendix 1 Table A1), early-season herbivore identity only affected the parasitoid community, but not the herbivore and predator communities (Supplementary material Appendix 1 Table A3). Aphid infestation on both plant populations predominantly increased the abundance of parasitoids associated with *Brevicoryne brassicae*, compared to plants with caterpillar infestation or no herbivores (see species score plots in Fig. 1–2, Supplementary material Appendix 1 Table A3).

Priority effects of order of arrival of early-season herbivores and specificity per plant population

In 2012 dual herbivore infestation had a different effect on the arthropod community than infestation with a single herbivore species, especially when aphids were present first. Community responses to early-season herbivores were comparable when aphids were feeding alone (A), simultaneously with caterpillars (A&C) or when aphid feeding was followed by caterpillar feeding (A–C) (Fig. 1, Supplementary material Appendix 1 Table A3). The reversed order of infestation, in which caterpillars were added first (C–A), and infestation by caterpillars only (C), differed from treatments in which aphids were added first (Fig. 1a–b, Supplementary material Appendix 1 Table A3). Parasitoids of the aphid *B. brassicae*, indicated by the number of aphid mummies found, were the strongest responder to the induction treatments. The parasitoids were more abundant in treatments in which aphids were present first. Interestingly, the aphid populations were not affected by the induction treatments and parasitoids thus did not follow a strict density dependent response to aphid population size (Supplementary material Appendix 1). The effects of herbivore treatment on community assembly were similar when only the responding parasitoid community was
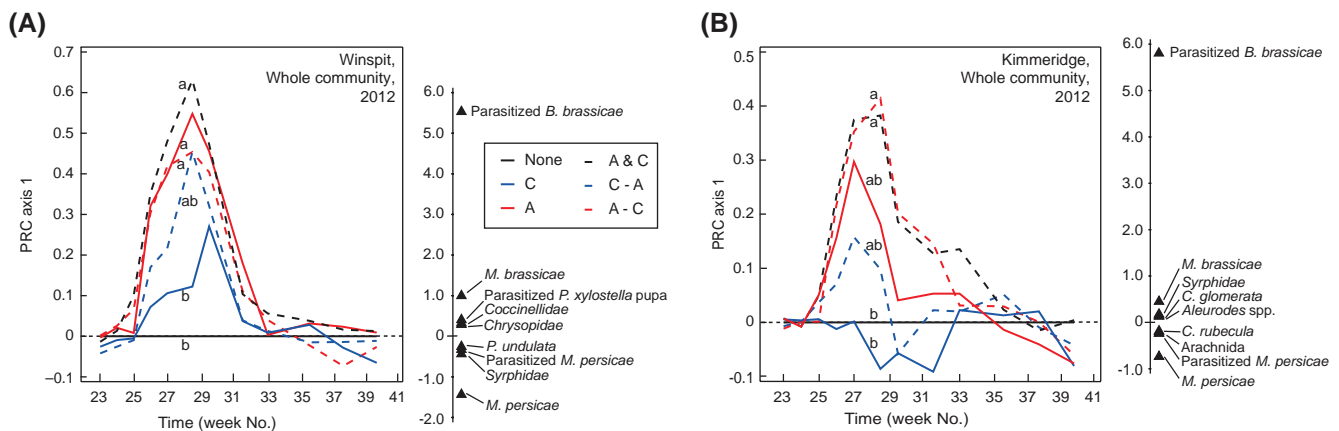

Figure 1. Principal response curves (PRC) showing the whole community development throughout the season. The first PRC axis over time is shown for (A) Winspit plants (WIN) and (B) Kimmeridge plants (KIM), and the species scores on the first ordination axis. Abundance of species high on this species score plot correlate with treatments with a high score on the first principal component axis for community composition, and *vice versa*. Only the nine most important species (most extreme (highest/lowest) ordination scores) are depicted, excluding *B. brassicae* and *P. xylostella* because their numbers are directly affected by experimental manipulation. Different letters denote significant difference between treatments on the response curve after pairwise comparisons. Early season herbivory treatments: None: no early season herbivore induction, set as baseline; C: caterpillar *P. xylostella*; A: aphid *B. brassicae*; A&C: aphid & caterpillar simultaneously; C–A: caterpillars, six days later followed by aphids; A–C: aphids, six days later followed by caterpillars. Cumulative explained variation of the first four principal component axes: 10.78% (WIN); 8.38% (KIM).
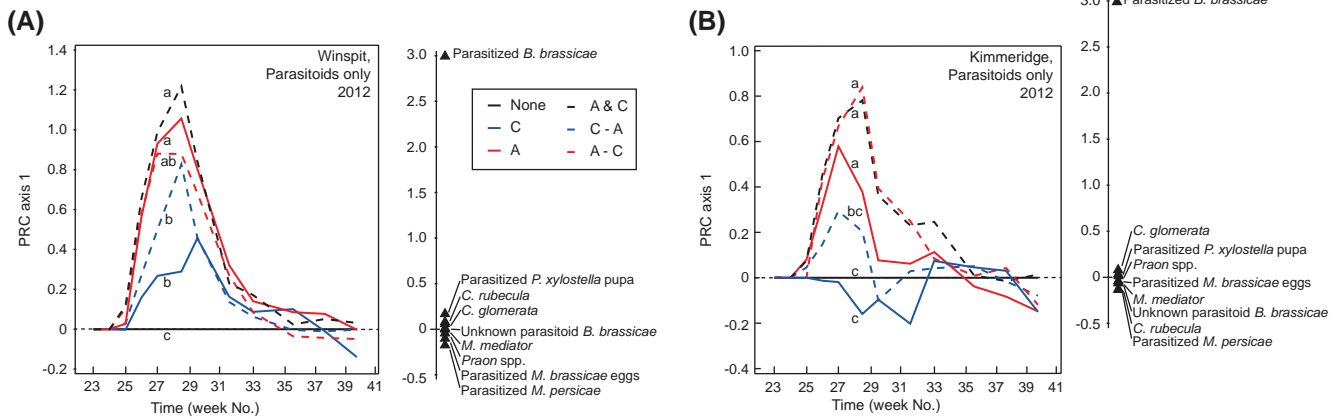
Figure 2. Principal response curves (PRC) showing the parasitoid community development throughout the season. The first PRC axis over time is shown for (A) Winspit plants (WIN) and (B) Kimmeridge plants (KIM), and the species scores on the first ordination axis. Abundance of species high on this species score plot correlate with treatments with a high score on the first principal component axis for community composition, and vice versa. All nine parasitoid species recorded are depicted. Different letters denote significant difference between treatments on the response curve after pairwise comparisons. Early season herbivory treatments: None: no early season herbivore induction, set as baseline; C: caterpillar *P. xylostella*; A: aphid *B. brassicae*; A&C: aphid & caterpillar simultaneously; C–A: caterpillars, six days later followed by aphids; A–C: aphids, six days later followed by caterpillars. Cumulative explained variation of the first four principal component axes: 22.72% (WIN); 19.05% (KIM).

considered, but effects of single or double herbivory in the first year (2012) did not differ from each other for the herbivore or predator community (Fig. 2a–b, Supplementary material Appendix 1 Table A3).

Since both identity of the added herbivore and dual herbivory with both caterpillars and aphids was important for the resulting arthropod community, we addressed whether the order of arrival of herbivores in the dual herbivory treatments modulated the development of the insect community differently. In both seasons, the insect community development was specific for the combination of effects of the order of arrival of the two early-season herbivores and the plant population on which they were found (significant double herbivore infestation treatment × plant population interaction; 2012: PRC, first axis explained 3.78%, Monte Carlo permutation test, pseudo-$F_{60,11}$: 19.8, p = 0.016; 2013: Table 1, Fig. 3). More specifically, in 2012, the community composition differed between the two plant populations (PRC, first axis explained 1.79%, Monte Carlo permutation test, pseudo-$F_{12,11}$: 10.1, p = 0.004), whereas this was not the case in 2013 (Table 1). In addition, the order of dual herbivore arrival itself did not result in significant effects on community development of the total arthropod community in either of the two years (Fig. 1, Table 1, Supplementary material Appendix 1 Table A3). However, especially in 2013, the assembly of the insect community strongly depended on the interaction between plant population and order of herbivore infestation (Supplementary material Appendix 1, Table A4). For example, in 2013 infestation of Kimmeridge plants with aphids followed by caterpillars (A–C) resulted in larger numbers of the generalist aphid *Myzus persicae* than other orders of herbivore infestation, but on Winspit plants the opposite effect was observed (A–C was colonised by fewer *M. persicae*

than found for other treatments; Fig. 3, species arrow for *M. persicae* is large in the direction of KIM A–C, but points away from WIN A–C).

Separate analyses of the effects on different functional groups (herbivores, predators, parasitoids; Supplementary material Appendix 1 Table A1) further revealed the specificity of community assembly on plant populations and the interactive effect with order of herbivore infestation. In 2012, only the parasitoid community was affected by the interaction between herbivore induction and plant population (PRC, first axis explained 10.71%, Monte Carlo permutation test, pseudo-$F_{60,11}$: 60.5, p = 0.002, Table 1, Fig. 2). To illustrate this, significantly more parasitized *B. brassicae* were found on Kimmeridge plants first induced by aphids (A–C) than on Kimmeridge plants first induced by caterpillars (C–A). In contrast, on Winspit plants, the order of herbivore infestation (C–A versus A–C) did not affect the parasitoid community.

In 2013 the specificity in interactions between order of herbivore infestation and plant population was found for the response of the herbivore community, but not the predator or parasitoid communities (Table 2, Supplementary material Appendix 1, Table A5). The time of the season also affected the response of the herbivore community in the second year, and this was different for the two plant populations and order of herbivore infestation. In the first half of the season in 2013, for example, the larvae of the specialist moth *Evergestis forficalis* were more abundant on Kimmeridge plants infested with caterpillars followed by aphids (C–A) than on Winspit plants with the same treatment (C–A) (Supplementary material Appendix 1 Fig. A1). Later in the season this effect disappeared (Table 1: no significant effect of treatments on herbivores in round 2).

Table 1. Results of partial redundancy analyses (partial RDA) on the arthropod community on plants induced with two herbivores in different orders of arrival. Early-season double herbivore inductions (A&C, A–C, C–A) in 2013 on two plant populations Kimmeridge (KIM) and Winspit (WIN), and their interaction were tested for significant differences. The first overall analysis including all arthropods, monitoring rounds and factors reveals a significant interaction term of induction treatment and plant population. The data is post-hoc further explored using RDA on subsets of the data to identify in more detail the species groups that are strong responders to plant population and induction treatment and the timing of these effects early or late in the season (monitored rounds). 'Induction+Plant population' explores the effects of both, but without their interaction effect. R1: data of the first round of observations in the field (week 21–25); R2: data of the second round of observations in the field (week 25–33). [a] Percentages show the % explained variation on the first RDA axis; [b] F-values are pseudo-F values of Monte Carlo Permutation test with subscripts of F-values (i,j) show the degrees of freedom (df) of explanatory variables (i) and covariates (j). Carnivores comprise both predators and parasitoids. Values in bold indicate significant effects.

| | | Factors tested | | | | | | | | | | | |
| | | Induction | | | Plant population | | | Induction + Plant population | | | Induction × Plant population | | |
Part of community	Monitored rounds	%[a]	F[b]	p	%	F	p	%	F	p	%	F	p
All arthropods	R1+R2	1.70	$F_{2,10}=1.2$	0.224	1.68	$F_{1,10}=1.4$	0.190	1.91	$F_{3,10}=1.2$	0.162	3.63	$F_{5,10}=1.4$	**0.024**
Herbivores only	R1+R2	1.63	$F_{2,10}=1.0$	0.446	2.21	$F_{1,10}=1.8$	0.094	3.00	$F_{3,10}=1.2$	0.234	5.33	$F_{5,10}=1.7$	**0.024**
Herbivores only	R1							3.65	$F_{3,4}=0.9$	0.532	9.81	$F_{5,4}=1.7$	**0.028**
Herbivores only	R2							4.08	$F_{3,6}=1.0$	0.414	7.89	$F_{5,6}=1.1$	0.296
Predators only	R1+R2							2.06	$F_{3,10}=1.0$	0.460	3.25	$F_{5,10}=1.1$	0.334
Parasitoids only	R1+R2							4.25	$F_{3,10}=1.4$	0.204	5.08	$F_{5,10}=1.0$	0.366
Carnivores only	R1+R2							2.96	$F_{3,10}=1.2$	0.234	3.78	$F_{5,10}=1.1$	0.354
Carnivores only	R1							2.63	$F_{3,4}=0.6$	0.898	6.30	$F_{5,4}=1.0$	0.482
Carnivores only	R2							6.79	$F_{3,6}=1.4$	0.164	11.51	$F_{5,6}=1.3$	0.162
On flowers	R1+R2	4.37	$F_{2,10}=2.1$	**0.032**	2.10	$F_{1,10}=1.7$	0.124	4.87	$F_{3,10}=2.1$	**0.016**	6.05	$F_{5,10}=1.7$	**0.022**
On flowers	R1							3.71	$F_{3,4}=0.8$	0.744	10.83	$F_{5,4}=1.4$	0.112
On flowers	R2							9.11	$F_{3,6}=1.8$	0.072	14.75	$F_{5,6}=1.7$	0.058
On leaves	R1+R2	1.16	$F_{2,10}=1.8$	0.686	1.70	$F_{1,10}=1.4$	0.180	1.98	$F_{3,10}=1.0$	0.456	3.37	$F_{5,10}=1.3$	0.112
On leaves	R1							3.91	$F_{3,4}=1.0$	0.426	10.50	$F_{5,4}=1.7$	**0.016**
On leaves	R2							3.09	$F_{3,6}=1.1$	0.372	4.95	$F_{5,6}=0.9$	0.578
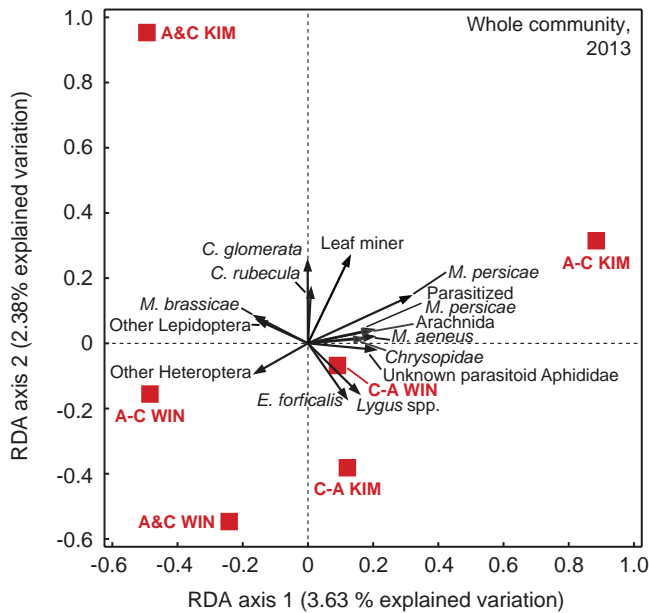
Figure 3. Partial redundancy analysis (partial RDA) showing the ordination of all species in the community and the order of early herbivore arrival × plant population interactions. The first two ordination axes are shown with squares indicating factors (order of early-season herbivore arrival × plant population interaction), and vector arrows indicating species ordination. Data of both monitoring rounds of the 2013 season is used. The 15 most important (longest arrows) species are shown, except *B. brassicae* and *P. xylostella* because their numbers are directly affected by experimental manipulation. Cumulative explained variation of the first four ordination axes: 8.19%.

Early-season herbivores and effect on leaf- or flower-associated insects

In 2013, the perennial *B. oleracea* plants flowered and developed seeds during the season. The arthropod communities on the vegetative (leaves) or on the reproductive (flowers) parts of the plants were differentially affected by the order of herbivore infestation on the leaves. Moreover, these effects were different for the two plant populations. To illustrate this, pair-wise comparisons revealed that the community composition on flowers differed on plants induced with caterpillars followed by aphids (C–A), compared to plants on which aphids and caterpillars had been introduced simultaneously (A&C) (Table 1, Fig. 4) (PCA, first axis explained 5.93%, Monte Carlo permutation test, pseudo-$F_{1,10}$: 3.2; p = 0.022; while A&C versus A–C: PCA, first axis explained 4.08%, Monte Carlo permutation test, pseudo-$F_{1,10}$: 2.0, p = 0.082; and A–C versus C–A: PCA, first axis explained 1.73%, Monte Carlo permutation test, pseudo-$F_{1,10}$: 0.9, p = 0.452). The response of the flower-associated community was also specific for both the order of herbivore infestation and the plant population (significant interaction effect between the two factors; Supplementary material Appendix 1 Table A6, Fig. 4), even though the communities did not differ between the plant populations
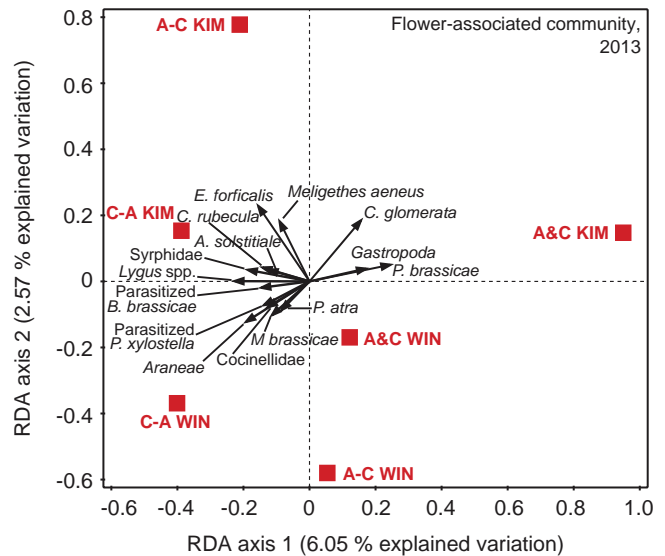

Figure 4. Partial redundancy analysis (partial RDA) showing the ordination of species of the flower-associated community and the order of early herbivore arrival × plant population interactions. The first two ordination axes are shown with squares indicating factors (order of early-season herbivore arrival × plant population interaction), and vector arrows indicating species ordination. Data of both monitoring rounds of the 2013 season is used, but only the species found on the flowering parts are included. The 15 most important (longest arrows) species are shown, except *B. brassicae* and *P. xylostella* because their numbers are directly affected by experimental manipulation. Cumulative explained variation of the first four ordination axes: 9.84%.

(Table 1). For example, caterpillars of *E. forficalis* and pollen beetles *Meligethes aeneus* were more abundant on flowers of Kimmeridge plants previously infested with caterpillars followed by aphids (C–A), than on Winspit plants that had been infested with the reversed order (A–C) or simultaneously infested with aphids and caterpillars (A&C; Fig. 4). In contrast, in 2013 the leaf-associated arthropod community was not affected by the order of herbivore infestation, the plant populations on which they were introduced, nor the interaction between the two (Table 1). Thus, in 2013 the flower-associated community, compared to the leaf-associated community, was more responsive to plant genetic background and differences in early season herbivores on those plants, even though early season herbivores were initially added to the leaves.

Seed set

The number of seeds collected at the end of the first reproductive cycle (2013) was not affected by the order of arrival of early herbivores (A&C, A–C, C–A; ANOVA F_2: 0.126, p = 0.882) or the plant population (ANOVA F_1: 1.252, p = 0.265), but a near-significant interaction effect between the two factors was observed (ANOVA F_2: 2.952, p = 0.055; Supplementary material Appendix 1 Fig. A2), indicating that the herbivore treatments have plant population-dependent effects.

Discussion

Historical contingency of herbivore arrival profoundly structures arthropod communities (van Zandt and Agrawal 2004, Viswanathan et al. 2007, Kessler and Halitschke 2007, Stam et al. 2014, Utsumi 2015). Here, we not only found that the identity of early-season herbivores from two different feeding guilds resulted in a different composition of the arthropod communities associated with these plants. We also show that infestation by a second herbivore modulated the community dynamics: simultaneous feeding by both a caterpillar and aphid early in the season differentiated arthropod community dynamics from effects caused by each herbivore individually. Moreover, the order of arrival of the two herbivores and the plant population on which the interactions occurred further differentiated community composition. Whereas in the first growing season the community changes were primarily represented by changes in the parasitoids associated with aphids, in the second season, when plants flowered, order of herbivore infestation affected herbivore communities, especially those herbivores feeding on the flowers. This indicates that priority effects of early-season order of herbivore arrival is an important component driving community assembly of arthropods on individual plants. Our study remained inconclusive with respect to the importance of these effects for plant fitness as the seed set was only nearly significantly different for the interaction term of plant population and herbivore treatment.

In the first and vegetative growth season of the plant, the predominant priority effects of herbivore arrival were reflected in the parasitoid community. In all treatments where the aphid *B. brassicae* was introduced first (A, A&C, A–C) abundance of its associated parasitoids increased. Because the introduced aphids were not removed and were introduced six days earlier than in the C–A treatment, these results may be derived from direct density dependent effects in which the introduced aphid population builds up to support a larger parasitoid community (Werner and Peacor 2003, Bukovinszky et al. 2008). These effects were not dampened when caterpillars were introduced simultaneously or a week after aphid infestation. However, when caterpillars were introduced first followed by aphids (C–A) fewer aphid parasitoids were found, despite the fact that the introduced *Brevicoryne brassicae* aphid population developed similarly on all treatments (Supplementary material Appendix 1). These findings suggest that direct density dependent effects were not the only factor explaining parasitoid populations. Caterpillar feeding on the plants may have altered the quality of the aphids and affected parasitoid populations through trait mediated effects (Ohgushi 2005). Aphid performance on caterpillar-induced plants may be poorer than on plants where aphids feed alone (Kroes et al. 2016, but see Soler et al. 2012) and may have resulted in smaller aphids that are less frequently parasitized by parasitoids (Bukovinszky et al. 2008). Moreover, caterpillar presence may hamper host location by aphid parasitoids (Ponzio et al. 2016). The outcome of herbivore–herbivore interactions as well as interactions with higher trophic levels may be herbivore density dependent (Ponzio et al. 2016, Pineda et al. 2017). In the second year, when plants flowered, infestation of the leaves with herbivores had consequences for the flower-associated community, but were weak and short term for the leaf-associated community. We recorded that during the first part of the season, order of early herbivory and plant population had the most profound effects on the composition of the leaf-associated herbivore community, after which effects diminished (Fig. 1–2, Table 1). A similar seasonal pattern was seen in another study with *B. oleracea* plants (Li et al. 2016), although others found season-long effects of early season herbivory (Viswanathan et al. 2005, Poelman et al. 2010, Utsumi 2015). Especially in a perennial system such as studied here, plant age can have large effects on arthropod–plant interactions (Lawrence et al. 2003, Quintero and Bowers 2011), and these effects may be driven by plant ontogenetic variation in defence and tolerance to herbivory (Boege and Marquis 2005).

Our data suggest that the first-arriving herbivore had the strongest effect on the further development of the insect community. Community responses to early-season herbivores were comparable when aphids and caterpillars were present together (A&C), when aphids were alone (A) or followed by caterpillars (A–C), and were different from a situation where caterpillars were introduced first (C–A). Although future studies would need to establish the mechanistic basis of these results, they concur with knowledge on plant phenotypic responses to sequential herbivore attack. Dual herbivory or single-herbivore infestation results in different plant responses, especially when those herbivores are of different feeding guilds (Zhang et al. 2009, Soler et al. 2012, Ali and Agrawal 2014), or arrive in different sequences (Voelckel and Baldwin 2004, Erb et al. 2011). Cross talk between plant phytohormone pathways that regulate responses to herbivory have been found to underlie plant phenotypic responses to sequential attack by aphids and caterpillars (Thaler et al. 2012). The salicylic acid (SA) pathway induced by aphids may interfere with plant responses to caterpillars that are regulated primarily through jasmonic acid (JA). SA-inducing aphids thereby reduce plant phenotypic responses to caterpillars, but the reverse effects of JA on SA are less pronounced (Zarate et al. 2007, Vos et al. 2013). When comparing only leaf chewers, other studies found that the first-arriving herbivore strongly determines plant resistance to other herbivores (Viswanathan et al. 2007, Stam et al. 2017), although subsequent herbivores have also been found to override effects of the first herbivores (Erb et al. 2011, Miller-Pierce and Preisser 2012). Plant plasticity in defence against herbivores may thus be an important mediator in directing the priority effects in community assembly on an individual plant.

According to the optimal defence theory, plant defence and responsiveness to herbivory should be highest in plant tissues with a high priority for plant fitness (McCall and Fordyce 2010), which might explain the significant effect of order of early season herbivore arrival cascading onto the

flower-associated community. This could be explained by different processes that are non-exclusive: 1) the physical movement of insects from leaves towards flowers as the season progressed, 2) systemic induction of phenotypic changes i.e. leaf herbivory causes phenotypic changes in the reproductive parts (McCall and Irwin 2006, Kessler and Halitschke 2009, Lucas-Barbosa et al. 2011, 2015), or 3) effects of induced plant phenotypic changes cascaded via consecutive community members up to species that are associated with flowers in a spatial-temporal manner (Utsumi et al. 2010). Herbivore feeding guilds have been found to differ in their effect on flower visitors (Rusman et al. 2018), and dual infestation of herbivores on the leaves may potentially further modulate these effects. Leaf-feeding herbivores may thereby strongly affect plant reproductive success when they affect arrival of herbivores that feed on flowers or seed pods (McArt et al. 2013) or interactions with pollinators (Kessler and Halitschke 2009, Lucas-Barbosa et al. 2011, 2015). In our study, we found that the impact on seed set was not significant and dependent on the plant population. This may indicate that the two plant populations differ in their defence strategy as well as their perennial reproductive strategy.

Closely related plant species have been found to differ in how they physiologically cope with two attackers, suggesting that plant-mediated interactions between herbivores are also a selective force on plant defence strategies (Agrawal et al. 2014, Ali and Agrawal 2014, Poelman and Kessler 2016). Here, we found a significant interactive effect of plant population and the order of herbivore arrival. This interactive effect may be due to variation in inducibility of traits that mediate indirect insect interactions between the populations of wild *B. oleracea* plants, such as the foliar concentration of glucosinolates (Gols et al. 2008, Newton et al. 2009) and the effect size of induced traits on insect community members (Li et al. 2014). We speculate that Kimmeridge and Winspit plants differ in SA–JA crosstalk (Kroes et al. 2016), which may result from selection by insect communities that differ in the order of herbivore arrival, or presence/absence of keystone species that subsequently affect a cascade of plant-mediated interactions (Keith et al. 2010, Utsumi et al. 2013, Stam et al. 2014, Poelman and Kessler 2016). When priority effects on individual plants are consistent across seasons, they may form an important selective regime on plant plasticity in defence as well as induced responses to herbivory (Poelman and Kessler 2016).

Our work shows that the order of herbivore arrival as part of arthropod community dynamics is a determinant of future season-long attack to plants and that these processes vary for plant populations. Not all community members were equally responsive to the inducing herbivores and the inducers themselves differed in how strongly they determined community dynamics. Historical contingency in plant–arthropod communities is therefore structured by priority effects of order and timing of species arrival. It is important to identify which community members shape the majority of species interactions as well as the predictability of historical

events (Chase 2003, Fukami 2015) to be able to infer the evolutionary consequences for individual community members (Urban and De Meester 2009), such as plant adaptations to deal with multi-herbivore attack (Poelman 2015, Poelman and Kessler 2016).

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