

Expansion of the winter moth outbreak range: no restrictive effects of competition with the resident autumnal moth

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Abstract. 1. Both direct and indirect competition can have profound effects on species abundance and expansion rates, especially for a species trying to strengthen a foothold in new areas, such as the winter moth (*Operophtera brumata*) currently in northernmost Finland. There, winter moths have overlapping outbreak ranges with autumnal moths (*Epirrita autumnata*), who also share the same host, the mountain birch (*Betula pubescens* ssp. *czerepanovii*). Competitive interactions are also possible, but so far unstudied, are explanations for the observed 1–3 years phase lag between the population cycles of the two moth species.

2. In two field experiments, we studied host plant-mediated indirect inter-specific competition and direct interference/exploitation competition between autumnal and winter moths. The experimental larvae were grown either with the competing species or with the same number of conspecifics until pupation. Inter-specific competition was judged from differences in pupal mass (reflecting lifespan fecundity), larval development time and larval survival.

3. Larval performance measurements suggested that neither direct nor indirect inter-specific competition with the autumnal moth reduce the growth rate of winter moth populations. Winter moths even had a higher probability of survival when reared together with autumnal moths.

4. Thus, we conclude that neither direct nor indirect inter-specific competition is capable of suppressing the spread of the winter moth outbreak range and that both are also an unlikely cause for the phase lag between the phase-locked population cycles of the two moth species.

Key words. Climate change, direct competition, indirect competition, invasion, phase lag.

INTRODUCTION

Ongoing global warming is known to facilitate the spread of new species especially to northern latitudes, where harsh winter temperatures have been a restricting factor

(Strathdee & Bale, 1998; Parmesan *et al.*, 1999; Bale *et al.*, 2002). In addition to temperature, a species spreading to new areas encounters many other abiotic and biotic factors, for example competition and predation, that might differ from the previously encountered conditions. Of these, competition has not yet been sufficiently studied regarding invasive species.

For the establishment of invasive species, both colonisation and competition are important factors (Duyck *et al.*, 2006). Competition theory states that shared resources, spatiotemporal co-occurrence and ecological similarity may all strengthen the competitive interactions between two species (Schoener, 1974). Therefore, competition with a closely related resident species in particular, can limit the spread of the newcomer. In general, if the effects of competition are asymmetric, one of the competing species might have a competitive advantage (Denno *et al.*, 2000; Kaplan & Denno, 2007; Long *et al.*, 2007). Moreover, the competitive interactions might lead to competitive exclusion, if inter-specific competition is stronger than intra-specific competition (Chesson, 2000). Consequently, if the resident and the invasive species do compete, the invasive species must be a better competitor and less affected by density to be able to spread to new areas. Earlier, inter-specific competition was not believed to be important for shaping insect herbivore communities (Hairston *et al.*, 1960; Connell, 1983), but more recent evidence shows that inter-specific competition can indeed act in shaping herbivore communities (Denno *et al.*, 1995; Kaplan & Denno, 2007).

Winter moth [*Operophtera brumata* (Linnaeus) (Lepidoptera: Geometridae)] has previously not occurred in high numbers in northern Finland, mainly because of low winter temperatures that were lethal for the moth eggs (Bylund, 1999; Jepsen *et al.*, 2008). Recently, however, the warming climate has allowed the winter moth to expand its geographical outbreak range from the northern coastal areas of Norway to more continental areas in northern Finland (Hagen *et al.*, 2007; Jepsen *et al.*, 2008; Klemola *et al.*, 2008). As a consequence, the winter moth has already caused visible defoliation and tree deaths of its main host plant, the mountain birch [*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti] in large areas of northernmost Finland and Norway far away from its earlier outbreak range (Tenow, 1972; Klemola *et al.*, 2007, 2008; Jepsen *et al.*, 2008). Furthermore, the more cold tolerant autumnal moth [*Epirrita autumnata* (Borkhausen) (Lepidoptera: Geometridae)], which also feeds on the mountain birch and has been reaching outbreak densities with severe large-scale forest defoliations and deaths for centuries (Tenow, 1972; Lehtonen, 1987; Haukioja *et al.*, 1988), can be found in the same region.

The autumnal and the winter moth have similar population dynamics and life cycles in northern Fennoscandia (e.g. Bylund, 1999). They both show cyclic fluctuations in population densities with 9–10 years between the peaks. Their eggs overwinter and

hatch in the spring synchronously with the birch bud burst. The larvae of both species live through five instars feeding on the same host plant and descend to the ground to pupate. Autumnal moths complete their larval stage approximately 1–2 weeks prior to winter moths (Mjaaseth *et al.*, 2005) and adults of both moth species mate and lay the eggs without feeding. Furthermore, the similar moth species are attacked by shared natural enemies, consisting of vertebrate and invertebrate generalists and hymenopteran parasitoids that lack other host alternatives in these areas (Ruohomäki *et al.*, 2000; Klemola *et al.*, 2002, 2009). Where the two species have already been known to coexist in the north, e.g. on some mountain slopes, they tend to prefer the opposite altitudinal extremes: autumnal moths having highest abundance in the medium and high altitudes, and winter moths being most common in the low and medium altitudes (Tenow, 1996; Mjaaseth *et al.*, 2005).

As a consequence of the similarities, autumnal and winter moths are bound to interact in all stages of their univoltine lifecycle. Inter-specific interactions could take place as direct interactions, in the form of interference or exploitation competition, and/or as indirect interactions. Both direct interference/exploitation competition and indirect competition via induced changes in the shared host plant (Denno *et al.*, 2000; Huntzinger *et al.*, 2008), can reduce the access of one species to resources. Such a limitation of resources can reduce the growth rate and hence significantly lower the rate of expansion, especially if it affects a newly expanding species (Harrison & Karban, 1986). Depending on the strength of the competition, this may result in a shift in the species' distribution range.

In areas where the outbreak ranges of autumnal and winter moths overlap, the population dynamics have often been observed to be phase locked, that is, coherent fluctuations, but with winter moth peak and trough densities lagging 1–3 years compared with those of autumnal moths (Tenow, 1972; Hogstad, 2005; Tenow *et al.*, 2007; Klemola *et al.*, 2008, 2009). A strong preference (or full specialization) of shared predators and parasitoids for one of the two moth species has been suggested as an explanation for the phase-lagged cycles of the winter moth (Klemola *et al.*, 2008, 2009). Also direct interference/exploitation competition and/or indirect competition via the shared host plant, represent two unexamined candidate mechanisms to explain the phase lag. If competition for the common food resource would constrain the population growth of winter moths, their densities might increase with a slower rate compared with the densities of the autumnal moth. Such a difference in population growth rates could result in an autumnal moth density peak preceding a winter moth density peak.

In this study, we experimentally examined the effects of indirect inter-specific competition via the shared host plant (hereafter simply referred to as 'indirect competition') and direct interference/exploitation competition (hereafter referred to as 'direct com-

petition') between winter and autumnal moths on larval growth and survival of both species under field conditions. We tested for both competitive scenarios to see if larval development time, larval survival and pupal mass (which is a direct correlate of fecundity in these moths; Haukioja & Neuvonen, 1985; Tammaru *et al.*, 1996; Klemola *et al.*, 2009) differ within species depending on whether individuals were grown in a single-species control or in a mixed-species experimental unit, which would imply differences between intra- and inter-specific competition. Our prediction was that winter moth larvae, as the invaders, would have a longer larval development time, higher mortality and/or reduced pupal mass when competing with autumnal moths compared with when growing up with only conspecifics. The experimental results were then used to hypothesise if the expansion of the winter moth could be restricted by the autumnal moth and also, if inter-specific competition could be responsible for the slower population increase of winter moths in the beginning of the cycle, causing the observed phase lag in the cycles of the two species.

MATERIALS AND METHODS

The field experiments for both direct and indirect competition were conducted simultaneously in a mountain birch forest in the immediate vicinity of the Kevo Subarctic Research Station (69°45'N, 27°01'E) during the summer 2008. The mountain birch is the dominant deciduous tree species in this area and is thus used by both of the moth species as a primary host.

For both experiments, the larvae of both species were haphazardly taken from a random set of small second instar larvae. Winter moth larvae were collected as neonates from Norway, approximately 50 km northeast from Kevo. Autumnal moths were taken from our lab stock, bred from field-collected larvae from the previous year. The different origin of the experimental larvae does not interfere with the studied question, as we compared the performance of larvae reared with individuals of the other species against the performance of control larvae reared with conspecifics from the same origin.

The collected winter moths were kept indoors to ensure growth, and thus might have been slightly bigger than they would have been under natural conditions when taken to the outdoors for the experiment. The autumnal moth larvae, however, were kept outdoors and were a similar size to the larvae occurring in nature. Larvae of both species were therefore approximately of similar size, whereas in nature, winter moth larvae grow a bit slower and might have been smaller than autumnal moths in the beginning of the experiment.

In both experiments, the general procedure of the field rearing was as follows. The larvae were allowed to feed undisturbed in branch-wide mesh bags (length 80–100 cm, width 35–50 cm) on trees growing in the forest for approximately 20 days. The indirect competition experiment preceded the direct competition experiment by 1 day for practical reasons. The start of the experiments was timed to match natural larval growth and mountain birch leaf elongation. Towards the end of the larval development period, all the mesh bags were checked daily and pre-pupating larvae that had ceased their feeding were collected and put in to 48-ml vials containing Sphagnum moss for pupation. Ten days after pupal formation, (hereafter pupation) the pupae were weighed to get an estimate of adult fecundity and their sex was identified. When all larvae had been collected from the trees, the percentage of feeding damage (further on simply called ‘defoliation’) in each mesh bag was visually estimated (as percentage of damaged foliage to the nearest 5%) and the mesh bags were removed. The development time was calculated as the thermal sum in DD2 (degree-days above the base of 2°C, which is close to the lower developmental threshold for autumnal and winter moths) of the pupation day minus the thermal sum in DD2 of the day when the larvae were put onto the trees (Ruohomäki *et al.*, 2003), thus covering the whole larval period on the trees. The temperature data needed for DD2 calculation were attained from the meteorological station located on the grounds of the Kevo Subarctic Research Station.

Indirect competition via the host plant

For the indirect competition (IC) experiment, 30 mountain birches were selected altogether within one large forest patch next to a gravelled forest road leading to the research station. The selected trees (height 3–5 m) were at least 10 m apart from each other and were divided into groups of three according to their location. For each group of trees, one randomly selected tree held two mesh bags with 20 winter moths each, one tree held two mesh bags with 20 autumnal moths each, and one tree held two mesh bags of which one had 20 winter moths and the other 20 autumnal moths (see Supporting information, Fig. S1 A). Thus, each tree experienced the same herbivore pressure in the beginning and the differences in density effects were minimized for the larvae. The larvae grew up with only conspecifics within their bag, but either with only conspecifics feeding on the same tree (single IC treatments for both species which were used as controls for the mixed IC treatment) or with larvae of the other species also feeding on the same tree (mixed IC treatment). The two mesh bags were placed closely together on the same ramet (mountain birch is a polycormic tree at the study area) to diminish possible differences in foliage quality between ramets or large branches (Suomela & Nilson, 1994). Overall, 600 autumnal and 600 winter moth larvae were placed on the trees.

Direct competition

For the direct competition (DC) experiment, 24 individual polycormic mountain birches (height 3–5 m) were selected on the other side of the gravelled forest road from the IC trees. Each tree was approximately 10 m apart from other trees and had three mesh bags placed on the same ramet. Each bag contained approximately 70 leaf buds in the beginning of the experiment to provide the same food quantity for each bag. The selected trees were randomly divided into three density groups (density treatment): low density trees had 10 larvae in each mesh bag, medium density trees had 20, and high density trees had 30 larvae in each mesh bag (see Supporting information, Fig. S1 B). For each tree in every density group, the three bags consisted of one bag with only winter moth larvae, one with only autumnal moth larvae and one with larvae of both species (see Supporting information, Fig. S1 B). In the mixed bags, half of the larvae were winter moth larvae, and half were autumnal moth larvae. Thus, in this experiment, larvae were always feeding with conspecifics and non-conspecifics on the same tree, but either had only conspecifics in the same bag (single DC treatments for both species which were used as controls for mixed DC treatment) or had non-conspecifics in the same bag (mixed DC treatment). A total of 720 autumnal and 720 winter moth larvae were placed in the mesh bags.

Statistical analyses

The effects of both direct and indirect competition on pupal mass and development time were analysed separately for both species with general linear mixed models (the procedure MIXED in SAS 9.1 statistical software SAS Institute Inc., Cary, USA) with random measurement designs. A bag was used as a random effect nested within a tree to take into account that larvae, reared in the same bag or tree, are not independent observations. In the IC experiment, the models included sex, IC treatment (single/mixed), defoliation and all their interactions as fixed effects. In the DC experiment, sex, DC treatment (single/mixed), density treatment (high, medium, low) and all their interactions were used as fixed effects. As random variables were included, the denominator degrees of freedom for the tests of fixed effects were computed using the method of Kenward & Roger (1997).

The effects of competition on survival were analysed for both IC and DC experiments with generalised linear mixed models (with the procedure GLIMMIX in SAS) with a binomial error structure and a logit link function. Odds ratios were used to assess the differences in effect sizes. For the IC experiment, species, IC treatment, defoliation and all their interactions were used as fixed effects and species, DC treatment, density treatment and all their interactions for the DC experiment. As in the general linear mixed models, a bag nested within a tree was included as a random effect.

For statistically significant effects, least-squares (LS) mean estimates for classifying factors or slope estimates for continuous factors are presented in the results with 95% confidence limits. For survival probability estimates, LS means and 95% confidence intervals were back-transformed from the logit scale.

RESULTS

Indirect competition

Altogether, 414 winter and 339 autumnal moth larvae pupated from the IC experiment and were taken into account in the statistical models. Detailed statistical results of the models can be found in the Supporting information (Table S1) for both species.

The pupal mass of winter moths was not affected by the feeding of non-conspecific larvae on the same tree (IC treatment: $F_{1,24.3} = 0.29$, $P = 0.59$; see Supporting information, Table S1 for the NS interaction terms). However, autumnal moth pupal masses in mixed trees decreased with increasing defoliation (IC treatment \times defoliation \times sex: $F_{1,310} = 4.34$, $P = 0.0381$, Fig. 1), with females reacting slightly more than males (slope comparisons: males *vs.* females in mixed: $F_{1,310} = 3.61$, $P = 0.0583$, single *vs.* mixed females: $F_{1,29.3} = 4.40$, $P = 0.0446$). This indicates negative effects for autumnal moth females when feeding on the same tree with winter moths.

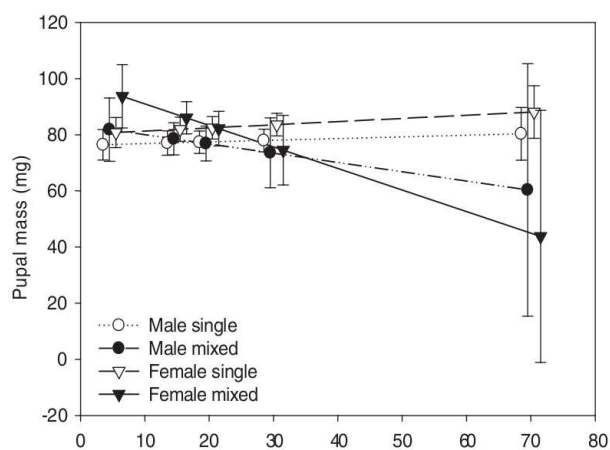


Fig. 1. Pupal masses of autumnal moth males and females growing on trees either with only conspecifics (single species) or together with winter moths (mixed species) in the indirect competition experiment. Least-squares means with their 95% confidence limits are shown for five different defoliation percentages using the 5th, 25th, 50th, 75th and 95th percentiles of the distribution. Lines illustrate the regression slopes. For illustration purposes the data points are slightly separated from each other at every percentile.

Defoliation in individual mesh bags affected winter moth pupal mass negatively ($F_{1,24.2} = 12.41$, $P = 0.0017$; slope -0.16 ± 0.17). All other explanatory variables for pupal mass were either included in the statistically significant three-way interaction

(concerning the autumnal moth) or were non-significant (see Supporting information, Table S1).

Growing in a mixed-species tree had no effect on winter or autumnal moth development time compared with growing in a single-species tree (IC treatment for winter moths: $F_{1,31.4} = 0.02$, $P = 0.88$; IC treatment for autumnal moths: $F_{1,35.9} = 0.08$, $P = 0.78$).

Survival probabilities differed between the two moth species (species: $F_{1,1130} = 9.18$, $P = 0.0025$) with winter moths being more likely to survive than autumnal moths (Odds ratio = 2.90, 95% CI = 1.46 – 5.80). Winter moths survived with a probability of 0.818 (95% CI = 0.731 – 0.882), whereas autumnal moths had a survival probability of 0.608 (95% CI = 0.491 – 0.713). However, the presence or absence of non-conspecifics in the same tree had no effect on moth survival in neither of the species (IC treatment: $F_{1,1130} = 1.43$, $P = 0.23$; IC treatment \times species: $F_{1,1130} = 1.82$, $P = 0.18$).

Direct competition

Overall, 448 winter and 435 autumnal moths completed their larval stage in the DC experiment, and were taken into account in the statistical models. As for the IC experiment, the details of the DC models for both species can be found in the Supporting information (Table S2).

The pupal masses of both species were affected by growing up in high densities, with autumnal moth females in single species bags reacting to density slightly more than moths in other groups (autumnal moth: density treatment \times DC treatment \times sex: $F_{2,402} = 5.61$, $P = 0.0039$; winter moth: density treatment $F_{2,41.1} = 8.47$, $P = 0.0008$). Autumnal and winter moth pupal masses were highest in the low density bags and lowest in the high density bags (Fig. 2A and B). However, the density treatment \times DC treatment interaction was not significant, suggesting that living together in the same bag with another species had no effect on the pupal mass of either species despite varying density (see Supporting information, Table S2). As some larvae died during the bag rearing, the initial differences in larval numbers between the density treatments might not have been represented by the numbers of larvae alive at the end of the larval period. However, although larval mortality was highest in the high density bags, the differences between the density treatment groups were still very clear at the end of the experiment (Fig. 2C).

Neither the DC treatment nor the density treatment had a significant effect on winter moth development time (DC treatment: $F_{1,50.6} = 3.39$, $P = 0.07$, density treatment: $F_{2,48.7} = 2.04$, $P = 0.14$). The development time of autumnal moths changed according to both density treatment and DC treatment (density treatment \times DC treatment: $F_{2,48.6} = 3.32$, $P = 0.0443$). In low and medium densities, development time was

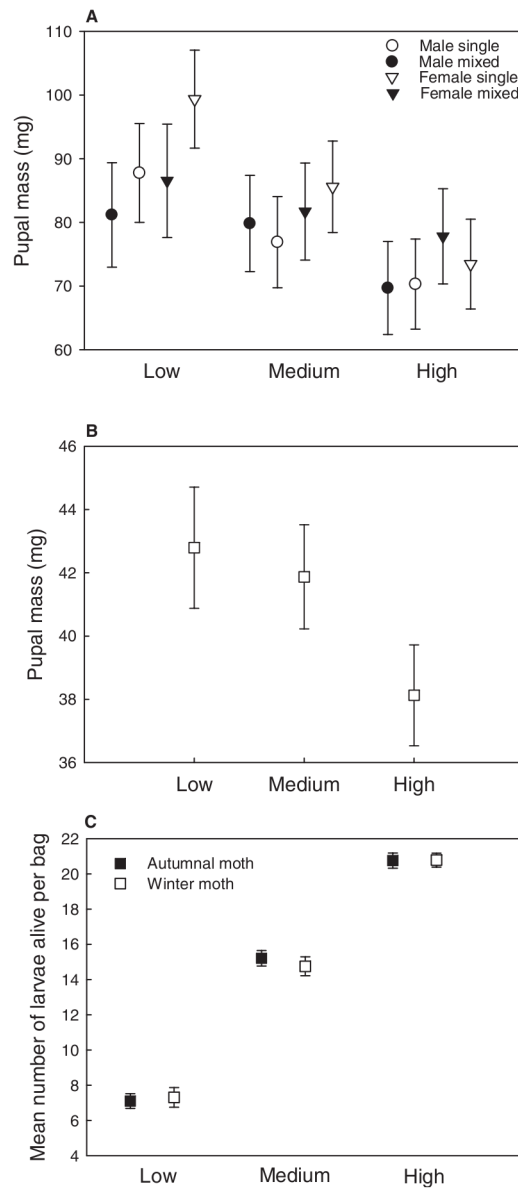


Fig. 2. Effects of larval density on the pupal masses of autumnal (A) and winter moths (B) in the direct competition (DC) experiment. Least-squares means with their 95% confidence limits are shown in both figures for low-, medium- and high-density groups. For autumnal moths, means are further separated according to sex and DC treatment (single/mixed). Mean numbers of larvae alive per bag in the different density treatments at the end of the larval period are also presented with 95% confidence limits for both species (C).

longer in the mixed-species treatment, but this was reversed in the highest density (Fig. 3).

The DC treatment affected the survival probabilities of the two species differently (DC treatment \times species: $F_{1,1385} = 12.15$, $P = 0.0005$, Fig. 4). Winter moths in mixed-species bags were much more likely to survive than winter moths in single-species bags [odds ratio (OR) = 2.63, 95% CI = 1.48 – 4.70], but there were practically no

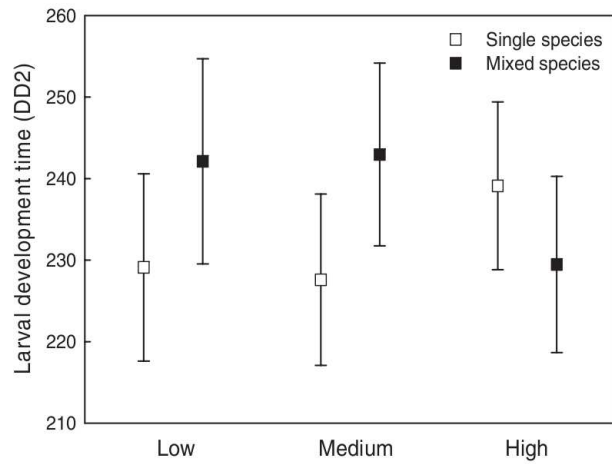


Fig. 3. Development time (in DD2) of autumnal moths in single- and mixed-species bags in different rearing densities in the direct competition (DC) experiment. Least-squares means with 95% confidence limits are shown.

differences in the survival of autumnal moth larvae in the different DC treatments (OR estimate = 0.98, 95% CI = 0.57 – 1.69).

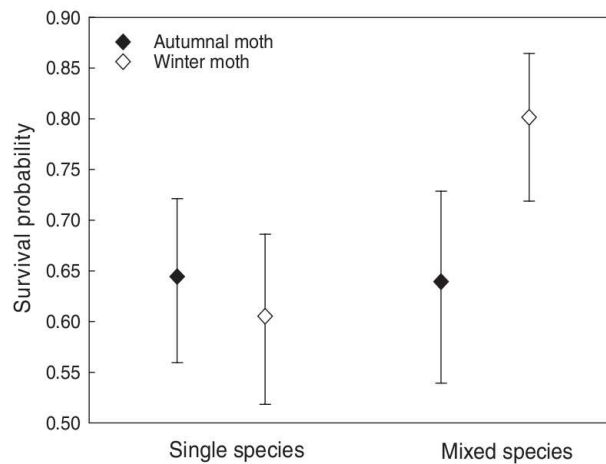


Fig. 4. Survival probabilities of winter and autumnal moths in single- and mixed-species bags in the direct competition (DC) experiment. Back-transformed least-squares means with 95% confidence limits are shown.

DISCUSSION

Our experimental findings on larval performance suggested that neither direct nor indirect competitive interactions with the autumnal moth reduce the growth rate of winter moth populations. In the direct competition experiment, winter moths even had a higher probability of survival when reared together with autumnal moths compared with rearing with conspecifics only. Accordingly, it seems clear that the inter-specific

competition is not capable of suppressing the spread of the winter moth outbreak range, and also that competition is an unlikely cause for the observed phase lag between the phase-locked population cycles of the two moth species.

Indirect host-mediated inter-specific competition, however, affected the resident species in a negative manner: pupal masses of the autumnal moth females were more strongly affected by defoliation when reared in the same tree with winter moths than with conspecifics only. Although an overall negative effect of defoliation could be expected (e.g. Ruohomäki *et al.*, 2003), this difference indicates some asymmetric effects of indirect competition via the host plant on the reproductive output, for the benefit of the invasive winter moth.

As with indirect competition, asymmetric effects can lead to direct competition affecting the spread and reproduction of one species negatively. Such a direct competition can occur as a result of both interference competition via behavioural interactions and exploitation competition via availability of the limiting resource. These alternatives, however, cannot be distinguished in our experimental design. As an indication of asymmetric direct competition effects in our study system, female autumnal moths had higher pupal mass when reared in single species bags compared with mixed species bags in low densities. In addition, winter moths survived significantly better when living in the same mesh bags with autumnal moths compared with winter moths living with conspecifics only.

Accordingly, the direct competition between species was not as strong as intra-specific competition for winter moths. Such a phenomenon of seemingly stronger intra-specific than inter-specific competition, might be a result of the particular behaviour of winter moths. Winter moth larvae tend to prefer feeding inside mountain birch leaves loosely spun together with silk threads (Tenow, 1972 and pers. obs. by authors). Consequently, winter moth larvae might compete with conspecifics for leaves in a situation where the amount of leaves is restricted (such as in our experimental design with closed mesh bags) and have more access to leaves when living with autumnal moths that browse from leaf to leaf. They might find leaves spun together by winter moths a less desirable food.

The negative effects of crowding are in accordance with previous studies on autumnal moths (Tammaru *et al.*, 2000; Ruohomäki *et al.*, 2003; Klemola *et al.*, 2008; Sillanpää, 2008). Our study also showed that winter moths seem to react negatively to crowding, but the effects between low and intermediate densities were negligible. Ruohomäki *et al.* (2003) showed that the effects of crowding on the autumnal moth start to take place at densities from 12.5 to 21 larvae per 100 short shoots. In our experiment, the original densities were c. 14.3, 28.6 and 43 larvae per 100 short shoots for low, intermediate and high density, respectively, equivalent to our 10, 20 and 30 larvae in

each mesh bag containing approximately 70 short shoots. Consequently, it seems that crowding does not affect winter moths until higher densities, 28.6–43 larvae per 100 short shoots, respectively.

In general, invasive species can dramatically affect the existing community, and the biotic interactions shaping it (Lodge, 1993; Sanders *et al.*, 2003; Tylianakis *et al.*, 2008). According to our study, the newly arisen situation, where winter moths also exhibit outbreak densities in northern Finland, is not likely to change as a result of competition. Furthermore, the results of this study suggest that the negative inter-specific competition effects inflicted on autumnal moths and higher tolerance of density effects, could lead to winter moths being better competitors overall. However, as has been previously reported (e.g. Bylund, 1999), autumnal and winter moths have been known to coexist in coastal areas in the north, but with slightly different altitudinal preferences. The competitive interactions reported in this study might partly explain the slight differences in altitudinal abundances, but it remains to be seen if a similar situation might be encountered soon in continental Finnish Lapland.

In both experiments, autumnal moths were the last to complete their development. This contradicts previous observations, according to which autumnal moths complete their larval period approximately 1–2 weeks before winter moths (Mjaaseth *et al.*, 2005). Although our experimental larvae might have been similar in size at the beginning of the experiments, as opposed to natural conditions with a possible size difference, this does not explain the differences observed in survival between the treatment groups in the direct competition experiment: here both autumnal and winter moths were more or less equally likely to survive in the single species bags. Neither does it provide an explanation for the negative effects of non-conspecifics feeding in the same tree on autumnal moth female pupal masses in the indirect competition experiment.

In conclusion, this was the first time that direct and indirect competitions have been studied between autumnal and winter moths in this northern system. Our field study could not find any evidence of competitive interactions reducing performance parameters of the winter moth. Winter moths seemed to be able to cope with a coexisting closely related species and appeared to be less affected by crowding than autumnal moths. Furthermore, the presence of winter moths seemed to have negative effects on the reproduction capacity of the autumnal moth. Consequently, it seems that neither direct competition with autumnal moths nor indirect competition via the host plant can reduce the growth rate of winter moths to such an extent that a further spread of the outbreak range could be impeded where climate is not a restricting factor. The examined competition types are not likely to be responsible for the phase lag in the population cycles of the two moth species, because negative effects on winter moth by the presence of the autumnal moth were not observed. It remains to be studied which

other factors in addition to predation and parasitism may contribute to the phase-lagged population dynamics of these moth species.

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SUPPORTING INFORMATION

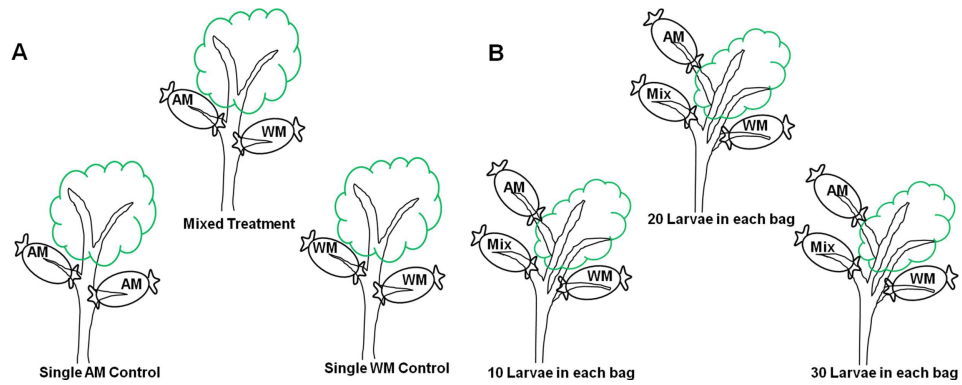


Figure S1. The experimental designs of indirect (A) and direct (B) competition experiments. Mesh bags contained autumnal moths (AM), winter moths (WM) or both (Mix).

Table S1. The results from all statistical models for the indirect competition (IC) experiment. Statistically significant results are in bold. Pupal mass and development time models were run for both species separately. Survival models included both species.

Explanatory variable	Autumnal moth			Winter moth			Both species	
	Pupal mass $F_{x,y}$	P	Development time $F_{x,y}$	Pupal mass $F_{x,y}$	P	Development time $F_{x,y}$	Survival $F_{x,y}$	P
IC treatment	2.64 _{1,26.5}	0.1160	0.08 _{1,35.9}	0.7843	0.5945	0.02 _{1,31.4}	1.43 _{1,1130}	0.2326
Defoliation	1.32 _{1,24.9}	0.2613	0.30 _{1,30.8}	0.5909	0.0017	0.00 _{1,31.3}	—	—
Sex	13.41 _{1,312}	0.0003	6.70 _{1,332}	0.0101	< 0.0001	3.36 _{1,395}	—	—
Species	—	—	—	—	—	—	9.18 _{1,1130}	0.0025
IC treatment × Sex	4.05 _{1,312}	0.0449	1.46 _{1,332}	0.2280	0.6933	0.85 _{1,395}	—	—
IC treatment × Species	—	—	—	—	—	—	1.82 _{1,1130}	0.1777
IC treatment × Defoliation	2.48 _{1,24.9}	0.1277	1.77 _{1,30.8}	0.1937	0.2846	0.17 _{1,31.3}	—	—
Defoliation × Sex	2.68 _{1,310}	0.1028	1.52 _{1,326}	0.2185	0.0618	0.91 _{1,396}	—	—
IC treatment × Defoliation × Sex	4.34 _{1,310}	0.0381	1.79 _{1,326}	0.1813	0.1082	1.20 _{1,396}	—	—

Table S2. The results from all statistical models for the direct competition (DC) experiment. Statistically significant results are in bold. Pupal mass and development time models were run for both species separately. Survival models included both species.

Explanatory variable	Autumnal moth		Winter moth		Both species	
	Pupal mass $F_{x,y}$	Development time P	Pupal mass $F_{x,y}$	Development time P	Survival $F_{x,y}$	P
Density treatment	9.47 _{2,40.4}	0.03 _{2,48.6}	8.47 _{2,41.1}	2.04 _{2,48.7}	0.47 _{2,1385}	0.6273
DC treatment	0.89 _{1,40.6}	1.89 _{1,49.4}	0.08 _{1,42.1}	3.39 _{1,50.6}	3.60 _{1,42}	0.0648
Sex	42.61 _{1,407}	5.15 _{1,426}	31.20 _{1,419}	23.61 _{1,430}	—	—
Species	—	—	—	—	5.33 _{1,1385}	0.0210
Density treat. × DC treat.	1.41 _{2,40.4}	0.2569	0.11 _{2,41.1}	0.26 _{2,48.7}	1.17 _{2,1385}	0.3119
Density treat. × Sex	0.75 _{2,402}	0.4754	0.87 _{2,416}	1.73 _{2,427}	—	—
Density treat. × Species	—	—	—	—	0.11 _{2,1385}	0.8972
DC treatment × Sex	1.84 _{1,407}	0.1754	0.12 _{1,419}	2.25 _{1,430}	—	—
DC treatment × Species	—	—	—	—	12.15 _{1,1385}	0.0005
Density treat. × DC treat. × Sex	5.61 _{2,402}	0.0039	0.39 _{2,416}	0.13 _{2,427}	—	—
Density treat. × DC treat. × Species	—	—	—	—	0.35 _{2,1385}	0.7070