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Population cycles of autumnal moth, *Epirrita autumnata*, in relation to birch mast seeding

Abstract We investigated the relationship between flowering peaks of the mountain birch, *Betula pubescens* ssp. *czerepanovii*, and population levels of the autumnal moth *Epirrita autumnata* in Ammarnäs, Swedish Lapland, during 1968–2000, and in Budal, Central Norway, during 1972–2000. There was a significant correlation between the two moth series, both of which showed three well-defined population cycles during the study period. In both areas, the population growth index of the moth was negatively related to population size, but also to the number of years since the previous flowering peak of mountain birch. In the northern study area, Ammarnäs, there was an additional positive effect of the winter temperature index, probably due to increased mortality of moth eggs during cold winters. No significant relationships were found between the number of birch female catkins and larval density in the previous 2 years. Both in Ammarnäs and in an area without moth outbreaks in south-eastern Norway, birch flowering was positively related to temperatures during flower bud formation and to the number of years since the previous flowering peak. The results support the idea of a lower content of chemical defence compounds in birch leaves after a mast reproduction, though we cannot exclude the possibility that the negative relationship between flowering and moth population levels was influenced or caused by stress associated with defoliation during moth outbreaks.

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Introduction

In Fennoscandia, there is a well-documented 9- to 10-year fluctuation in the numbers of autumnal moth, *Epirrita autumnata* (Lepidoptera: Geometridae), feeding on mountain birch, *Betula pubescens* ssp. *czerepanovii* (Tenow 1972). Even though the autumnal moth is also common at lower altitudes, outbreaks are restricted to the alpine or arctic birch forest zone. The most important factors regulating the population of this moth species appear to be larval growth and survival (Tammaru et al. 1996). The decrease in larval performance after a population peak coincides with chemical changes in birch leaves and, therefore, a delayed induced defence mechanism in host plants has been suggested to be the ultimate cause for the moth population cycle (Haukioja 1980, 1991; Neuvonen and Haukioja 1984; Kaitaniemi et al. 1998). This hypothesis requires that the induced resistance relaxes after some years, allowing a new population growth of moths.

Kaitaniemi et al. (1999) found that birch trees maintained leaf biomass after defoliation the previous year, at the expense of growth and reproduction. Hence, during a moth outbreak, birch reproduction may remain low until the moth population has declined. The annual seed crop of birch varies considerably (Perala and Alm 1990), but to our knowledge there are no long-term studies of the relationship between birch flowering and caterpillar density. Even though birch reproduction is likely to be influenced by moth outbreaks, herbivory alone is unlikely to explain the large annual fluctuations in seed production. This is because mast seeding (mast=high seed crop in a plant population) is also observed in birch stands at lower altitudes (Perala and Alm 1990), where outbreaks of pest insects are rare.

Mast seeding is common among forest trees in general (Silvertown 1980), but the advantage of this reproduc-

tive strategy is not well understood (Kelly 1994). If individual plants are forced to flower in synchrony because of climatic constraints, intraspecific competition may make it advantageous to maximise seed production, at the expense of other activities, in mast years (Selås 2000a). Since vegetative growth is actually low in mast years (e.g. Silvertown and Lovett-Doust 1993), there may also be a trade-off between seed production and chemical defence (e.g. Bazzaz et al. 1987; Bergelson and Purrington 1996; Baldwin et al. 1998). That population outbreaks of some cyclic herbivore species coincide with post-mast years of their host plants (Selås 1997, 1998, 2000b; Selås and Steel 1998) supports this view. Such outbreaks may result in serious defoliation and thus prolong the periods needed for plants to recover between each mast.

In southern Norway, most population outbreaks of autumnal moth started after a mast year of Norway spruce, *Picea abies*, which has been reported to flower in synchrony with mountain birch (Selås 1997). Because this analysis was based on subjective reports, and few data on birch flowering were available, the result should be regarded only as indicative for further studies. In this paper, we use data from two long-term investigations to analyse the growth rate of the autumnal moth population in relation to mast years of mountain birch, as well as the flowering of mountain birch in relation to moth density. In addition to biotic factors, winter weather may also influence growth rates of the autumnal moth, because low temperatures ($<-35°C$) are detrimental for the eggs (Tenow 1975; Tenow and Nilssen 1990; Virtanen et al. 1998). For the birch, flowering and seed production are influenced by temperatures in spring and during flower bud formation in the previous year (Perala and Alm 1990). We therefore included temperature indices in our analyses.

Materials and methods

The data were obtained from two unmanaged subalpine birch forests, one in Ammarnäs, Lycksele lappmark, Swedish Lapland (65°58′ N, 16°03′ E), and one in Budal, Sør-Trøndelag County, central Norway (62°45′ N, 10°30′ E). The Ammarnäs area is situated 540–720 m above sea level, and the Budal area, 780–900 m above sea level. In Ammarnäs, most birch forests are of the rich "meadow" type, whereas in Budal, oligotrophic "heath" birch forests predominate. The investigations in Ammarnäs are part of the so-called LUVRE-project (Enemar et al. 1984). More detailed descriptions of the study areas are given by Andersson and Jonasson (1980), Enemar et al. (1984) and Hogstad (1997).

From Ammarnäs, temperature data were only available from spring and early summer (15 May–15 July). As a temperature index for the winter period (December–March) and the period of flower bud formation (July–September), we therefore used the North Atlantic Oscillation (NAO) index, which is an alternation in atmospheric pressures over the Atlantic Ocean, strongly related to interannual variation in temperatures in the northern hemisphere (Hurrell 1995). In Norway and Sweden, there is a positive covariation between the NAO index and winter temperatures (Hurrell and Van Loon 1997). In Budal, we found a significant positive correlation between the NAO index and the mean temperature both in December–March ($r=0.59$, $n=29$, $P<0.001$) and in July–September ($r=0.48$, $n=27$, $P=0.012$).

The density of autumnal moth caterpillars has been investigated annually since 1968 in Ammarnäs, and since 1972 in Budal. In Ammarnäs, caterpillars were counted within four 50×50 m areas, three situated in meadow birch forests and one in a heath birch forest (see Andersson and Jonasson 1980). Within each area, caterpillars were counted at 1,000 randomly selected short shoots, all available from the ground, six times in each plot during the last 2 weeks of June. An annual index of larval density was calculated by first taking the mean number of larvae found per 1,000 shoots in each of the four areas, and then the mean value for the four areas. In Budal, caterpillars were collected at random from the lowest 4 m of birch branches using a sweep-net. Each year, 5–15 collections, each of 100 sweeps, were taken in the first days of July, when the larvae were in their fourth to fifth instars. The annual index from Budal then is the mean number of larvae of instars 4 and 5 collected per 100 sweeps.

Because of the exponential nature of population growth, we used the natural logarithms of the moth series rather than the real indices when we analysed moth populations in relation to birch flowering. The Budal series, which contained several years where no caterpillars were found, was ln(x+1) transformed to meet the assumptions of normal distribution. We tested for cyclicity in the transformed series using the Fisher kappa test in a spectral analysis (Fuller 1978). The transformed series were thereafter detrended using the first difference. The new indices correspond to the growth rate of the moth populations. These detrended series did not differ from a normal distribution (Shapiro-Wilk test; Ammarnäs: $W=0.96$, $P=0.37$; Budal: $W=0.97$, $P=0.66$).

In Ammarnäs, the fluctuation in birch catkin occurrence has been investigated since 1979. Prior to 1979, years with superabundant birch flowering were reported by Enemar et al. (1984). During 1979–1988, the number of male and female catkins was counted at marked branches of 60 birches, 20 from each of three different plots within the study area. The selected branches were those growing between a lower and a higher mark on the stem, and they were all available from the ground. Because the vitality of the selected trees gradually decreased, another method was used from 1988, and thus the indices from the two periods are not directly comparable. For the latter period, a branch from each of 25 birches in each of eight study plots was selected randomly, and the total number of catkins was counted on 20 shoots of each of the selected branches. The branches were selected from a distance at which catkins were not visible. In the analysis of birch flowering in relation to moth number, the female catkin index from 1979–1988 was multiplied by a factor so that the number counted in 1988 corresponded to that obtained by the new method introduced that year.

Birch catkins have not been counted in Budal, but years with superabundant birch flowering have been reported by Hogstad (1996). However, superabundant flowering may not necessarily result in high seed production. For both study areas, we therefore present data on the breeding density of redpoll, *Carduelis flammea*, a species which feeds to a large extent on birch seeds and whose numbers are expected to peak after a high seed production (data from Enemar et al. 1984; Hogstad 1996; O. Hogstad, unpublished data; A. Enemar, personal communication). The redpoll is nomadic, i.e. it occurs at high density in areas with rich food supply. If birch seeds are produced in abundance, they will be available for the redpoll throughout the winter, and in spring huge amounts can be found on the ground. Peak densities of redpoll are therefore expected to lag 1 year behind the peaks in mountain birch seed production.

We tested for relationships between indices of moth populations and birch flowering by a stepwise multiple-regression procedure. First we used the detrended ln-transformed moth series (moth growth rate) as response variables and the number of years since the previous peak in birch flowering as explanatory variable. Additional predictor variables were the winter temperature index and the untransformed moth index of the previous year, because of the assumption of density dependence. Thereafter we used the annual number of female catkins counted in Ammarnäs as response variable and the total number of caterpillars counted in the 2 pre-

ceding years (see Kaitaniemi et al. 1999) as explanatory variable. To control for any effects of temperatures during flower bud formation and flowering, we included the temperature index of July–September in the previous year and of June in the current year as explanatory variables. Based on the assumption of resource storage between mast years (Kelly 1994), we also used the number of years since the previous flowering peak as a predictor variable.

To compare the results from the analysis of birch flowering in Ammarnäs with those from an area without moth outbreaks, we conducted a similar test for a data series on seed production of birch (*B. p. pubescens* and *B. pendula*) from Vestfold County, south-eastern Norway. In this area, an annual index for seed production has been calculated from subjective evaluations made by foresters and published in a Norwegian journal of forestry during 1927–1957 (e.g. Eide 1928). This index, which corresponds to that used for spruce by Selås (1997), was used as the response variable in a stepwise regression model with the mean temperature in June in the current year, the mean temperature in July–September in the previous year, and the number of years since the previous peak in seed production as predictor variables.

None of the explanatory variables used in the regression analyses were significantly correlated. With an α-to-enter or α-to-remove at 0.10, forward and backward procedures gave the same results. The residuals did not differ significantly from a normal distribution in any of the selected models. An important assumption in linear regression is that the residuals are uncorrelated. Because of a significant autocorrelation at time lag 4 in the Ammarnäs moth series ($r=-0.50$, $P=0.003$), we tested the assumption of uncorrelated observations by fitting autoregressive models (up to order four) to the residuals from the selected regression models. None of these autoregressive models were significant.

Results

The ln-transformed moth series differed significantly from a purely random process (Ammarnäs: Fisher's kappa=10.65, $P<0.001$; Budal: Fisher's kappa=9.88, $P<0.001$), with a well-defined periodogram peak for a period of approximately 11 years in Ammarnäs and 10 years in Budal. There was a significant correlation between the two ln-transformed series ($r=0.65$, $n=29$, $P<0.001$), and also between their growth rate (first difference; $r=0.38$, $n=28$, $P=0.045$). Both populations went through three cycles during the study period, with one peak in the mid 1970s, one in the mid 1980s and one in the mid 1990s (Fig. 1). The last peak occurred, however, somewhat earlier in Ammarnäs than in Budal. Thus, a new population increase could be observed in the last 2 years of our study period in Ammarnäs, but not in Budal.

In Ammarnäs, there were peaks in birch flowering in 1967, 1970, 1980, 1985, 1989 and 1998, and in Budal in 1970, 1974, 1980, 1991 and 1992 (Fig. 1). The flowering peak in Budal 1970 was confirmed by Aaheim (1971, 1973a, 1973b), who reported the flowering of mountain birch in Sør-Trøndelag County to be excellent in 1970, fair in 1971 and poor in 1972. Except from Ammarnäs in 1986, the redpoll population usually reached high levels after a year with superabundant birch flowering (Fig. 1), confirming that seed production was indeed high in most of these years.

The common flowering peaks of 1970 and 1980 occurred prior to the first and second moth population cy-
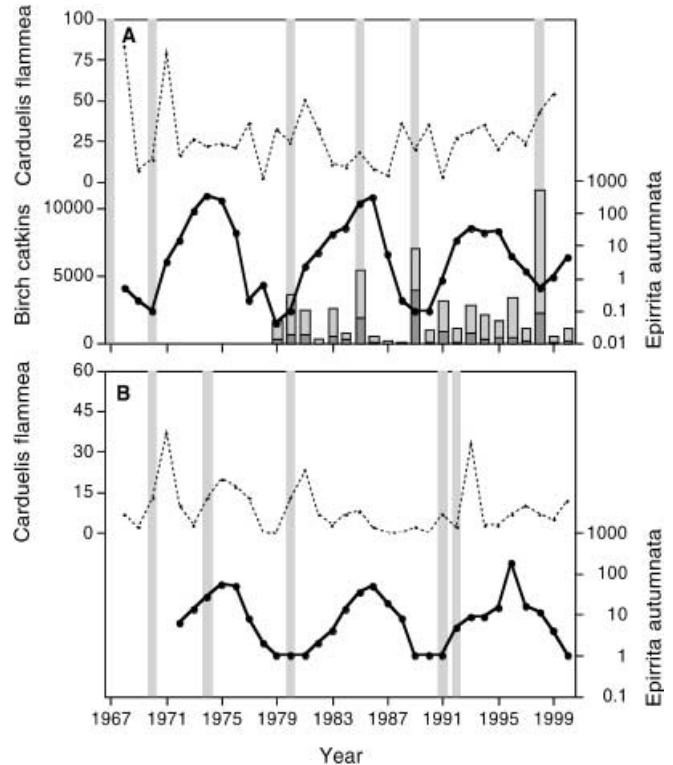

Fig. 1 Annual fluctuation in the number of autumnal moth larvae (*filled circles*, *solid curves*, logarithmic axis) in relation to birch flowering in two alpine birch forests: Ammarnäs, northern Sweden (**A**) and Budal, central Norway (**B**). Years with a peak in birch flowering are *hatched*. In Ammarnäs, birch catkins were counted during 1979–2000 (*dark bars* female catkins, *light bars* male catkins). Because of different methods used during 1979–1988 and 1988–2000, the bars from the former period have been enlarged by 75%, to equalise the 1988 index (female and male catkins pooled) obtained by the old method with the number counted by the new method introduced that year. Prior to 1979, superabundant birch flowering was reported in 1967 and 1970 (Enemar et al. 1984). From both areas, the population index (pairs per km^2) of the seed-eating redpoll, which is expected to peak in number after a year of high seed production, is shown by a *dotted curve*. Data from Ammarnäs are from Enemar et al. (1984) and A. Enemar (personal communication)

cles (Fig. 1). Prior to the third population cycle, there was a flowering peak in 1989 in Ammarnäs and in 1991–1992 in Budal (Fig. 1). In Ammarnäs, there was a new peak in birch flowering in the late 1990s, prior to the last 2 years with an increase in the moth population (Fig. 1).

In both study areas, the annual growth rate (first difference) of the autumnal moth populations decreased with increasing population level and with increasing time period since the previous peak in birch flowering (Table 1). All results were significant except for that of flowering peaks in Ammarnäs. However, if there was high seed production only when a flowering peak was followed by a high redpoll population, i.e. not in Ammarnäs in 1985 (Fig. 1), the relationship between moth growth rate and the number of years since the previous peak in seed production was highly significant also for

Table 1 Results from a stepwise regression model for each study area, with the first difference of the ln-transformed autumnal moth indices as response variable. For Ammarnäs, the winter temperature index is the North Atlantic Oscillation (December–March), which is an alternation in atmospheric pressures over the Atlantic Ocean, strongly related to interannual variation in temperatures in the northern hemisphere. A partial R^2 is given for explanatory variables that were entered into the model. Sample size is number of years

Explanatory variable	Ammarnäs (n=33)		Budal (n=29)	
	R^2	P	R^2	P
Temperature index, December–March	0.15	0.048	–	0.380
Number of caterpillars in the previous year	0.10	0.044	0.22	0.004
Number of years since last peak in birch flowering	0.08	0.068	0.18	0.011
Selected model	0.33	0.009	0.41	0.002
Adjusted R^2	0.26		0.36	

Table 2 Results from stepwise regression models with the annual number of female catkins counted (Ammarnäs, 1979–2000; Fig. 1) or an estimated seed index (Vestfold, 1935–1957; Fig. 2) as response variable. In Ammarnäs, the rich birch flowering in 1985 was not followed by a high population of the seed-eating redpoll (Fig. 1), and therefore this year was omitted from the analysis. For Ammarnäs, the temperature index of late summer is the North Atlantic Oscillation (July–September). A partial R^2 is given for explanatory variables that were entered to the model. Sample size is number of years

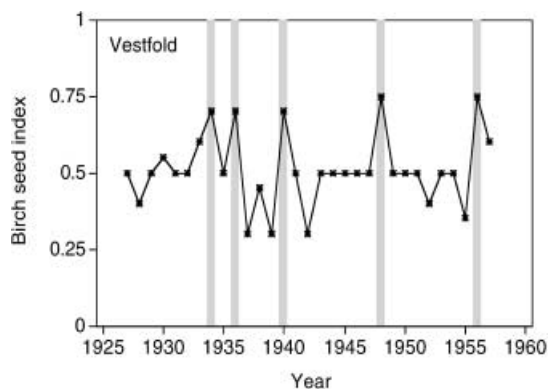| Explanatory variable	Ammarnäs (n=21)		Vestfold (n=23)	
	R^2	P	R^2	P
Number of caterpillars in the 2 previous years	–	0.664		
Number of years since last peak in birch flowering	0.19	0.038	0.09	0.049
Temperature index, July–September in the previous year	0.20	0.017	0.29	0.007
Temperature index, June in the current year	–	0.173	0.20	0.001
Selected model	0.39	0.019	0.58	<0.001
Adjusted R^2	0.32		0.52	

Fig. 2 Annual fluctuation in birch seed production in Vestfold County, south-eastern Norway, where moth outbreaks do not occur. Years regarded as peak years in the statistical analysis are *hatched*. The seed index was calculated from subjective estimates given by foresters, and published annually in a Norwegian journal of forestry. A seed index of 0.5 corresponds to medium seed production

this study area (Partial R^2=0.30, P=0.001). In Ammarnäs, but not in Budal, there was also a significant positive effect of the winter temperature index (Table 1). The result from Budal was the same whether mean temperature or the NAO index was used as predictor variable.

The mean annual number of female birch catkins counted in Ammarnäs could not be explained by larval density in the 2 preceding years (P=0.853), or by the number of years since the previous flowering peak (P=0.361). There was, however, a tendency for a positive association with the July–September temperature index in the previous year (R^2=0.16, P=0.078). This result was significant if 1985 (with no succeeding peak in the redpoll population) was not regarded as a peak flowering year and was omitted from the analysis, because there was then also a positive relationship between the number of birch catkins and the number of years since the previous flowering peak (Table 2). A similar result was obtained for the birch seed index from Vestfold 1935–1957 (Fig. 2), but here there was also a positive relationship with the mean temperature in June (Table 2).

Discussion

Despite the large distance between the study areas (approximately 450 km), the two moth populations tended to fluctuate in synchrony. The two first population cycles reported were apparently common for large parts of northern Norway and Sweden (Ehnström et al. 1974, 1998; Löyttyniemi et al. 1979; Austarå et al. 1983; Harding et al. 1998), indicating that the cycles are initiated by some environmental factor that operates at a large-scaled landscape level. Because forest trees require a minimum sum of temperature during summer for flower bud formation, climate has commonly been assumed to be responsible for the geographical synchrony in seed production. If the reproductive strategy of the birch is

actually the key factor for understanding moth cycles, then the latter should also be expected to show significant geographical synchrony.

Most peaks in birch flowering occurred when the population densities of the autumnal moth were low and, therefore, the number of years since the previous peak contributed to explaining the growth rate of the moth. Population growth was also negatively related to the population level of the previous year, indicating that some direct density-dependent mechanisms, such as competition, predation or parasitism, were important. In Ammarnäs, but not in Budal, there also seemed to be a negative effect of cold winters. A likely explanation for the difference between the study areas is that Budal is situated farther south, and also closer to the coast, so that winter temperatures less often reached levels low enough to kill moth eggs.

In both areas, there was a peak in birch flowering in 1970 and 1980. In Ammarnäs, there was a marked increase in moth population growth in the succeeding years 1971 and 1981, whereas in Budal, population growth was not apparent until 1982 (no data from 1970–1971). For the unsynchronised birch flowering prior to the third population peak, there was a similar delay in the moth response in Ammarnäs. Neither of the two delays could be explained by low winter temperatures. There is however the possibility that, e.g. in 1990, moth eggs in Ammarnäs suffered from a shorter period with low winter temperatures, not reflected by the NAO index. Caterpillars of cyclic Lepidoptera species such as the autumnal moth may also be influenced negatively by other temporal weather conditions, such as high temperatures in spring and summer (Haukioja et al. 1985; Watt and McFarlane 1991; Virtanen and Neuvonen 1999; Selås 2000b). Furthermore, the generally low number of moths found in years with low population levels may bias the calculated growth rates more than those calculated from periods with higher population levels.

In addition to the flowering peaks observed prior to each population cycle, there was good flowering in Budal in 1974, and in Ammarnäs in 1985. These flowering peaks occurred close to the peaks in larvae number. However, a rich flowering does not necessarily result in a high seed crop, or in seeds of high quality. In fact, the redpoll population in Ammarnäs was not high in 1986, as would have been expected had there been a rich supply of birch seeds. The flowering peak in Budal in 1974 was followed by a peak in the redpoll population, though not as high as in 1971, 1981 and 1993. In 1974, spring temperatures were unusually high, and this may have had a positive influence on flowering and seed production in Budal that year (see Perala and Alm 1990).

We found no significant relationship between the number of female catkins and larval density in the 2 preceding years. As for the birch seed index from Vestfold, where moth outbreaks do not occur, there appeared rather to be an effect of temperatures during flower bud formation and of the number of years since the previous flowering peak. Hence, factors other than herbivory seemed to be important for annual seed production even in Ammarnäs. However, we might have obtained other results if data on seed production, and not only on flowering, had been available. Then, there might also have been a significant relationship with June temperatures, as found for the birch seed index from Vestfold.

The positive relationship between birch flowering in Ammarnäs and the number of years since the previous flowering peak with a high redpoll population would be expected if resource storage is involved in mast seeding, but also if defoliation caused by moth outbreaks modifies the periodicity of masting. The tendency for longer intervals between peak years in Ammarnäs than in Vestfold could be due to lower primary productivity as a result of lower temperatures and/or stress caused by moth outbreaks. Kaitaniemi et al. (1999) found that birches on which a 75% defoliation had been performed in the 2 preceding years had a lower proportion of short shoots with female catkins than control trees, while trees with only 25% defoliation did not differ from controls. The question then is if the defoliation observed in Ammarnäs was serious enough to significantly affect birch flowering. The moth outbreak in the 1990s was rather weak compared to the former population peaks.

Herbivore population cycles are most pronounced at high altitudes and latitudes, i.e. in areas with low temperatures, where the risk of serious plant damage during the outbreaks is also highest. In Budal, the birch forest was not harmed to any great extent during the moth peaks, whereas in Ammarnäs, the two first outbreaks resulted in partial defoliation. Interestingly, there were also lower temperatures in general during the 1970s and 1980s than during the 1990s. In Budal, the only serious defoliation reported was in the early 1940s (J. Hindbjørg. personal communication), when temperatures in general were low. These observations are in accordance with the study of Virtanen and Neuvonen (1999), who found that larval survival and egg production of the autumnal moth were highest when temperatures were low.

Virtanen and Neuvonen (1999) assumed that low parasitoid activity at lower temperatures was important for the higher performance of the autumnal moth. Another possible explanation is that plant performance is reduced at low temperatures. Lower primary production combined with reduced availability of minerals when soil temperatures are low may reduce the ability of plants to respond to increased levels of herbivory. The defence ability of the host plant may in turn influence the viability of the herbivores, and thus their vulnerability to natural enemies.

Population outbreaks of moths feeding on trees are often restricted to old stands, or, at least, the larval density is highest in old stands (Bylund 1997; Ruohomäki et al. 1997). This is in accordance with the idea of seed production as the driving force behind the cycles, because old trees, with lower future reproductive value, should be expected to invest more in each reproduction than young trees, and thus be more vulnerable to subsequent herbivore attacks.

Our focus on the possible impact of birch mast seeding on the population growth of the autumnal moth does not mean that possible effects of moth outbreaks on birch reproduction should be ignored. Even though our suggestion is that birch masting is responsible for the moth outbreaks, herbivory is likely to reduce seed production between masts and prolong the intermast periods. An alternative explanation for the observed relationships between birch flowering and moth outbreaks is that the variation in seed production is determined mainly by larval density, i.e. that the interaction type is "top-down" rather than "bottom-up". If so, the geographical synchrony must be due to factors operating directly on the moths or their enemies, and not on the birches. A third possibility is that both birch masting and moth outbreaks are largely determined independently by a third factor. As our data cannot be used to distinguish between these alternatives, future studies should focus on the impact of birch masting on the chemical composition of birch leaves and thus on larval performance.

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