Masting and trophic cascades: interplay between rowan trees, apple fruit moth, and their parasitoid in southern Norway

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Satake, A., Bjørnstad, O. N. and Kobro, S. 2004. Masting and trophic cascades: interplay between rowan trees, apple fruit moth, and their parasitoid in southern Norway. – Oikos 104: 540–550.

We analyzed berry production in rowan, *Sorbus aucuparia* L., in southern Norway and examined the ramifying effects of rowan masting on the dynamics of the dominant seed predator and its parasitoid. The apple fruit moth, *Argyresthia conjugella* Zeller, is a pre-dispersal seed predator of rowan. The larva of the apple fruit moth rely on rowan berries, which in turn is attacked by the parasitoid wasp, *Microgaster politus* Marsh. We found classic masting in rowan: berry production varied across years (the mean coefficient of variation = 1.02) and was spatially synchronized at large scale (the averaged correlation coefficient = 0.67). Berry production represented a two-year cycle in western but a three-year cycle in eastern Norway. The abundance of the moth and the parasitoid also varied across years and were spatially synchronized. The degree of spatial synchrony decreased and cyclicity became obscure with increasing trophic level. We attempted to assess two different components to the predator satiation, functional and numerical satiations, based on a simple population dynamics model. The observed pattern of seed predation testified that both of functional and numerical satiations were at work in this system. In a comparison at different locations, rowan trees with more variable berry production were more effective in reducing losses to the seed predator. The parasitoids also seemed to experience satiation through the fluctuation in their host abundance. These results show that rowan masting has an adaptive foundation, which impacts the dynamics of higher trophic levels.

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Variable and synchronous seed production by plant populations has been reported across a broad group of tree species (Herrera et al. 1998). This phenomenon is called masting, or mast seeding (Kelly 1994, Kelly and Sork 2002). A number of studies focus on identifying and estimating the evolutionary advantages of masting. The two best supported hypotheses consider how masting enhances the survivorship of seedlings by satiating seed predators (the "predator satiation hypothesis", Janzen 1971, Silvertown 1980, Nilsson and Wästljung 1987) or, for wind pollinated trees, how masting

improves pollination efficiency (Nilsson and Wästljung 1987, Smith et al. 1990, Kelly et al. 2001). Masting by sympatric taxa that share seed predators can also increase the predator-swamping effect of masting and generate amplified fluctuations in consumer abundance (Shibata et al. 1998, Kelly et al. 2000).

Several theoretical studies of masting have identified potential mechanisms that individual trees may employ to achieve variable reproductive effort that is synchronized among individuals. Non-linear (thresholded) allocation of energy reserves in combination with pollen

limitation has recently been shown to provide a theoretically plausible physiological mechanism underlying masting dynamics (Isagi et al. 1998, Satake and Iwasa 2000, 2002a). Empirical studies have confirmed the impact of climatic fluctuations (such as temperature and precipitation level) correlated across large scale on spatial synchrony in seed production even in the absence of pollen limitation (Koenig and Knops 1998, 2000, Koenig et al. 1999, Rees et al. 2002, Schauber et al. 2002). When pollen limitation and external environmental forcing are at work in concert, the degree of spatial synchrony is further enhanced and maintained at a high level (Satake and Iwasa 2002b). Spatially synchronous and temporally variable seed set is a common phenomenon that is – at least crudely – accounted for by ecophysiological mechanisms.

The community consequences of masting are, in contrast, only known for selected case studies. The pulsed reproductive efforts may impact the dynamics of seed predators (Liebhold et al. 2000, Selås et al. 2001). Mice and squirrels, for instance, experience enhanced survival and rapid population growth in years of oak masting, but these populations may conversely crash to low levels in years with few acorns because of a shortage of food resources (Wolff 1996, McShea 2000). Such population fluctuations in rodents triggered by masting has been shown to have cascading effects through food webs, inducing outbreaks of gypsy moth and human risk of Lyme exposure (Ostfeld et al. 1996, Ostfeld and Keesing 2000). Trophic cascades are particularly likely to occur in food chains involving specialized seed predators and their natural enemies.

This paper reports the analysis of a spatiotemporally extensive data-set of one such system. Berry production in rowan, Sorbus aucuparia L., has been reported to vary substantially between years in a geographically synchronized fashion (Sperens 1997a,b, Kobro et al. 2003). The apple fruit moth, Argyresthia conjugella Zeller, is a predispersal seed predator (parasite) whose larvae rely on rowan berries. The larva of the apple fruit moth in turn is often attacked by the parasitoid wasp, Microgaster politus Marsh. (Ahlberg 1927, Kobro et al. 2003). We examine the ramifying effects of rowan masting on the dynamics of the seed predator and its parasitoid, by analyzing the spatiotemporal data of the annual berry production in rowan, the infestation level of the seed predator, and the level of parasitism of the moth larva in southern Norway.

We focus on three interrelated issues: (1) temporal ramification of masting – how temporal variability and cyclicity in berry production is transferred to upper trophic levels (2) spatial ramification of masting – how spatial synchrony in berry production is transferred to upper trophic levels, and (3) adaptive foundation of masting – evidence of predator's (or parasitoid's) satiation through the trophic interaction. In detecting

predator (or parasitoid) satiation from the data, we distinguish two mechanisms: "functional" and "numerical" satiations. Functional satiation is caused by the satiation of predator's feeding capacity. Numerical satiation, in contrast, originated from the amplified fluctuation in consumer abundance caused by masting- if the number of the predators is reduced by a very small seed production in a previous year, the predator population as a whole cannot cope with a great increase in seed production. Using a simple population dynamics model, we illustrated how these two satiation mechanisms are closely related, and how we can analyze these mechanisms in the data.

Material and methods

Study site and species

To optimally control apple fruit moth infestation of apple orchards, the Norwegian Crop Research Institute, Plant Protection Center, initiated a program to monitor moth abundances and forecast outbreaks on apple (Edland 1978). The program has monitored rowan seed set, apple fruit moth abundance, and abundance of the moth's chief parasitoid at 60 to almost 150 locations across southern Norway for the 21 years spanning 1979–1999 (the monitoring is still ongoing but our analysis will embrace these first two decades). Being a service program, the geographical location varied somewhat. However 45 locations have been consistently monitored during the entire period (Fig. 1).

In Scandinavia, rowan, S. aucuparia, is the most common tree in a group of very similar congeners (Lid 1987). Reproductive individuals vary greatly in size from tall shrubs (1–2 m) to full sized trees (> 2 m). The clusters of white flowers are produced in the early summer, and ripen to conspicuous red berries in the fall. Flower and berry production vary greatly between years in a spatially synchronous manner conforming to the classic notion of masting (Sperens 1996, Kobro et al. 2003). Each individual tree produces anywhere from 0 to > 100,000 berries in a given year.

The rowan berries and/or seeds are important resources for at least three seed predators: two phytophagous wasps (Megastigmus brevicaudis Ratz. the rare Haplocampa alpina Zett.) and the apple fruit moth (A. conjugella). The apple fruit moth, which is distributed across much of boreal Eurasia and North America, is the most important pest of apple in Scandinavia (Ahlberg 1927). The primary and preferred host of the apple fruit moth is rowan (or congeners such as Sorbus intermedia, Ahlberg 1927). However, when rowan mast is low relative to the moth abundance, many female moth individuals switch host and invade apple orchards, causing significant economic loss (Ahlberg 1927, Sperens 1997a,b). In other years moth populations are fully
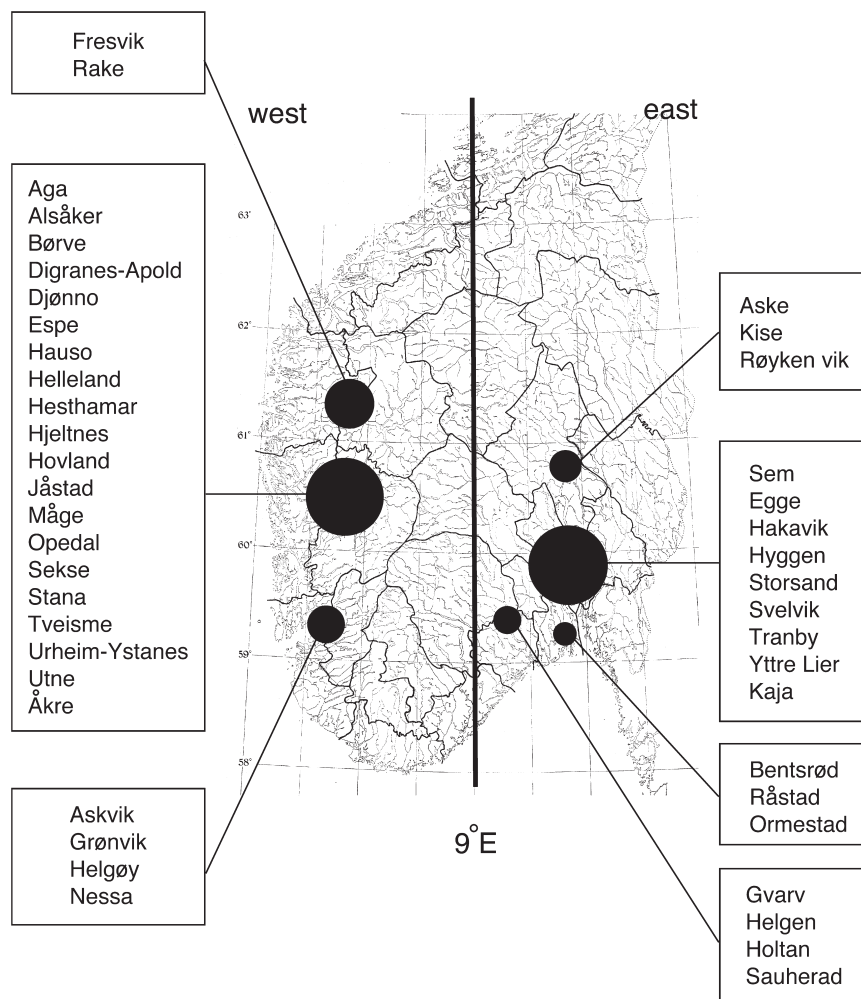
Fig. 1. Map of southern Norway showing the locations of study sites. Western Norway (longitude < 9°E) includes 26 and eastern Norway (longitude > 9°E) includes 19 sites.

Fresvik
Rake

west   east

Aga
Alsåker
Børve
Digranes-Apold
Djønno
Espe
Hauso
Helleland
Hesthamar
Hjeltnes
Hovland
Jåstad
Måge
Opedal
Sekse
Stana
Tveisme
Urheim-Ystanes
Utne
Åkre

Aske
Kise
Røyken vik

Sem
Egge
Hakavik
Hyggen
Storsand
Svelvik
Tranby
Yttre Lier
Kaja

Bentsrød
Råstad
Ormestad

Askvik
Grønvik
Helgøy
Nessa

9°E

Gvarv
Helgen
Holtan
Sauherad

confined to the primary host. The adults lay eggs in the newly initiated rowan berries. The larva hatches after 2 weeks. Once fully grown, the larva leaves the berry to pupate in the ground beneath the tree (Sperens 1997a). The larvae are parasitized by at least three parasitoids (two ichnemonids and one braconid, Ahlberg 1927). Of these, the solitary braconid wasp, *M. politus*, appears to be the dominant parasitoid on the apple fruit moth.

are estimated by counting the number of lepidopterous pupae and hymenopterous cocoons appearing from the moth larvae at the end of the incubation period. The abundance of the moth for a given year and site was calculated as the number of berry clusters multiplied by the infestation rate. Similarly, the abundance of parasitoids was calculated by the moth abundance multiplied by the level of parasitism.

Monitoring program

Agricultural advisers counts the number of berry clusters on reference branches or reference trees in the vicinity of orchards. To estimate the infestation level by apple fruit moth, 1000 berries are sent from each site to the program coordinator (Sverre Kobro), who incubates them and counts the number of apple fruit moth larvae emerging from these. The percentage of parasitoid larvae

Temporal variability

Annual fluctuation in berry production was examined for each location using the coefficient of variation CV = σ/μ, where σ is the standard deviation and μ is the mean seed production at the individual level. To calculate a 95% confidence interval, we resampled the time series data repeatedly with replacement (1000 permutations) and erected confidence intervals in the bootstrap dis-

tribution of CV. We used the same approach to quantify the unertainty of abundance of the apple fruit moth and the prasitoid.

In plants exhibiting mast seeding, seed crop size is reduced in years following mast years. This results in negative autocorrelation at lag 1 or 2 in time series of seed production (Norton and Kelly 1988, Sork et al. 1993, Koenig et al. 1994). We used the standard autocorrelation analysis to quantify the ACFs (auto-correlation functions) for each time series. ACFs were similarly calculated for each time series of the moth and parasitoid abundances.

Spatial synchrony

To asses synchrony among sample locations, we calculated the correlation coefficient, $\rho_{i,j}$, between the time series at location i and j. The mean synchrony across the entire region (i.e. the degree of regional synchrony) is calculated by averaging $\rho_{i,j}$ over all pairs of locations,

$$\bar{\rho} = \frac{1}{n(n-1)} \sum_i \sum_{j \neq i} \rho_{i,j}$$

where n is a total number of locations (i.e. n = 45). We constructed a 95% confidence interval by drawing the random sample of the locations with replacement and recalculating $\bar{\rho}$ (Bjørnstad et al. 1999). This procedure was repeated 1000 times to erect bootstrapped confidence intervals in the bootstrap distribution of $\bar{\rho}$. The same approach was used to measure regional synchrony for the upper trophic levels (the apple fruit moths and their parasitoids).

The spatial correlation function (SCF) decomposes regional synchrony as a function of distance (Bjørnstad et al. 1999). The expected correlation coefficient, $\rho_{i,j}$, between time series at locations i and j separated by distance $d_{i,j}$ is governed by the function $\rho(d)$, which is the SCF. We estimated the SCFs from the time series data to each of the three trophic levels by applying the non-parametric correlation function (Bjørnstad and Falck 2001). We generated bootstrapped confidence envelopes around the SCFs by resampling the locations with replacements and then repeated this process 1000 times to give a bootstrap sampling distribution for SCF (Bjørnstad and Falck 2001).

Predator satiation

There are two different mechanisms inducing predator satiation: (1) "functional satiation" – if predator's feeding capacity has an upper threshold, predators are satiated by a large seed production (Holling 1959); and (2) "numerical satiation" – if the number of the predators is reduced by a very small seed production in

a previous year, the predator population as a whole cannot cope with a great increase in seed production, resulting in a small fraction of seeds predated. Using a simple model, we will illustrate how these two satiation mechanisms are closely related, and how we can analyze these in the data.

Let the amount of berries produced and the number of the adult's predator in year t be B(t) and N(t). When adults of the predator have a functional response f(B(t)), the fraction of attacked berries is given by f(B(t))N(t)/B(t). If adults of the predator randomly attack berries and single larva emerges from the berry attacked, the number of adults of the predator in the next year, N(t + 1), will be

$$N(t+1) = cB(t)\left[1 - \exp\left(-\frac{f(B(t))N(t)}{B(t)}\right)\right] \qquad (1)$$

where c is a survival rate of the larva. The proportion of berries predated in year t is:

$$P(t) = 1 - \exp\left(-\frac{f(B(t))N(t)}{B(t)}\right) \qquad (2)$$

If f(B(t)) linearly rises with B(t), there is no satiation in the functional response and P(t) is independent of B(t). If f(B(t)) is given by the type II function that rises nonlinearly with B(t) towards the maximum attack rate, the functional response is:

$$f(B(t)) = \frac{aB(t)}{1 + bB(t)} \qquad (3)$$

In such a case, P(t) decreases with B(t) (Eq. 2), meaning that larger seed production reduces losses to predation – the "functional satiation". In addition, P(t) increases with N(t) (Eq. 2). This positive relationship between P(t) and N(t) is considered as the "numerical satiation" – the proportion of berries attacked will be low when the abundance of the predators is low. In this way, the proportion of berries attacked results from the interplay between the functional and numerical satiations. Our aim is to assess both mechanisms in the data. Our data provide estimates of the proportion of berries predated, $\hat{P}(t)$, and the amount of berries produced, $\hat{B}(t)$. Substituting $\hat{P}(t)$ and $\hat{B}(t)$ in Eq. 2, we have

$$N(t) = -\frac{\hat{B}(t)}{f(\hat{B}(t))}\log(1 - \hat{P}(t)) \qquad (4)$$

From Eq. 1 and Eq. 4, we obtain

$$\log(1 - \hat{P}(t)) = -\frac{f(\hat{B}(t))}{\hat{B}(t)}\hat{B}(t-1)\hat{P}(t-1) \qquad (5)$$

$1 - \hat{P}(t)$ in Eq. 5 represents the proportion of "healthy" (un-predated) berries. If f(B(t)) is given by Eq. 3, log(1 − $\hat{P}(t)$) increases with $\hat{B}(t)$, which means that the proportion of berries predated, $\hat{P}(t)$, decreases with $\hat{B}(t)$. Hence we can assess the functional satiation by testing for a

positive relationship between $\log(1 - \hat{P}(t))$ and $\hat{B}(t)$. The product $\hat{B}(t-1)\hat{P}(t-1)$ in Eq. 5 represents the amount of berries predated in year $t-1$, which is proportional to the number of adult predators in year t (Eq. 1). Numerical satiation is, thus, assessed by testing for a negative relationship between $\log(1 - \hat{P}(t))$ and $\hat{B}(t-1)\hat{P}(t-1)$ – the proportion berries predated, $\hat{P}(t)$, increases with the amount of berries predated.

For simplicity, we will rewrite Eq. 5 as

$$z(t) = g(x(t-1), \; y(t)) \qquad (6)$$

where $x(t-1) = \hat{B}(t-1)\hat{P}(t-1)$, $y(t) = \hat{B}(t)$, and $z(t) = \log(1 - \hat{P}(t))$. Then, to visualize whether $z(t)$ shows negative dependence on $x(t-1)$ and positive dependence on $y(t)$, we estimated the 2-dimensional function, $g(x(t-1), \; y(t))$, by applying a 2-dimentional thin-plate spline (Wood 2001). We also computed partial Spearman's rank correlations to test the direction and strength of the relationships.

We also used the method that is often applied to examine the predator satiation (Kelly and Sullivan 1997, Shibata et al. 1998). If the level of predation depends on the population size of predators as controlled by seed production in previous years, the fraction of berries attacked and seeds consumed will depend on the ratio of berry production in the previous year relative to the current year (Kelly and Sullivan 1997, Shibata et al. 1998). A bad fruiting year that followed a good fruiting year will experience enhanced predation (and vice versa) through the numerical response of the predator. To assess this, we examined the predation level (i.e. the proportion of attacked berries) as a function of year-to-year ratios in berry production. Numerical satiation will lead to a negative correlation between the proportion of berries attacked and the year-to-year ratio in berry production. This was investigated by logistic regression. However, any functional satiation can potentially induce a spurious relationship between attack rate and the current/previous ratio of seed set. We therefore employ a randomization test that should be robust to such spurious interdependencies to test the significance of the relation: we sampled pairs of amount of berry produced and proportion of berries predated, and calculated the year-to-year ratios for these randomized data set (1000 randomizations). Significance of the logistic regression was assessed on the basis of these randomized relations.

A third test that is rarely provided is an intra-specific test of predator satiation. The predator satiation hypothesis predicts that the more variable populations should attain the higher overall seed survival (Janzen 1971, Waller 1979, Silvertown 1980). To assess this, we examined the total proportion of seeds lost to predation as a function of temporal variability in seed production, measured by CV. In each location, total proportion of seed predated was calculated by dividing the total

number of predated seeds by the total number of seeds produced over the 21 years. We, again, used logistic regression to examine how predator escape is a function of the CV.

To understand the analogous relationship between the seed predator and its parasitoid, we also examined the patterns of "parasitoid" satiation. We applied the sequence of methods discussed above considering the abundance of the moth larvae as the fluctuating food resources for the parasitoid. Since it is plausible to assume each attacked berry includes a single larva (Ahlberg 1927), the abundance of larvae is given by the amount of attacked berries, $\hat{P}(t)\hat{B}(t)$. To visualize the functional and numerical satiations of the parasitoid, we estimated the 2-dimensional function for the proportion of healthy larvae by applying a 2-dimentional thin-plate spline. Partial Spearman's rank correlations was also computed to test the direction and strength of the relationships. We plotted the proportion of moth larvae parasitized as a function of the year-to-year ratio of the moth larva abundance. The relationship was fitted by using logistic regression and significance was tested by using a randomization test.

The procedure has been implemented in the R language (www.r-project.org). We used the net library as freely available from the authors (onb.ent.psu.edu/onb1/) and the gam library to estimate the non-parametric correlation function and the 2-dimentional smoothing spline.

Results

Temporal variability

The berry production in rowan fluctuated across years (Fig. 2A). The coefficient of variation, CV, in berry production at each location ranged from 0.67 (boot-strapped 95% confidence interval 0.50–0.82) to 1.63 (bootstrapped 95% confidence interval 1.00–1.98) with a mean of 1.02 (SE = 0.03). The abundance of the apple fruit moth and the parasitioid also fluctuated across years (Fig. 2B, C) with mean CV of 0.96 (SE = 0.03) and 1.16 (SE = 0.05) respectively.

The results of autocorrelation analysis for berry production of rowan showed a conspicuous division between geographical region. We therefore separated the study sites into two groups: western Norway (longitude < 9°E) and eastern Norway (longitude > 9°E, Fig. 1). In western Norway, the means of autocorrelations showed positive values at lags 2, 4, 6, and 8 and negative values at lags 1, 3, 5, and 7 (Fig. 3A), testifying to a 2-year cycle in the berry production. In contrast, the trees in eastern Norway exhibited the positive means of autocorrelations at lags 3, 6, and 9 and negative ones at lags 1, 2, 4, 5, 7, 8, and 10 (Fig. 3D). Thus rowan had a 3-year fruiting cycle in eastern Norway with some
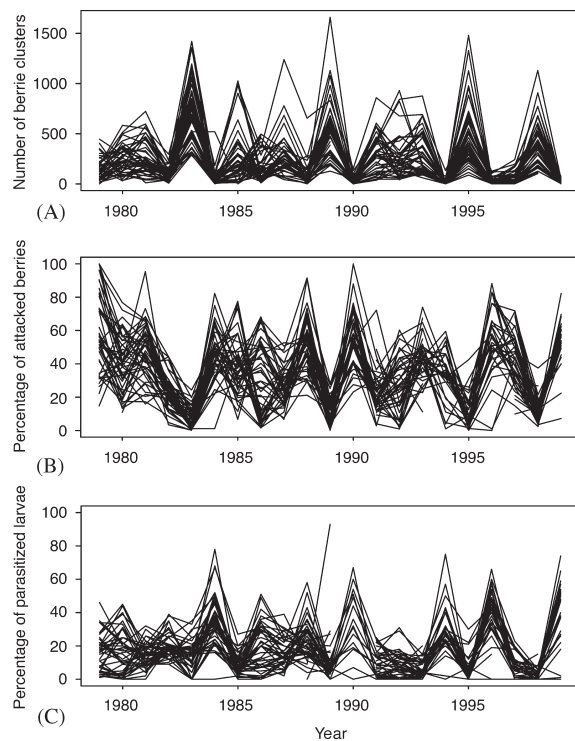
Fig. 2. Time series data of (A) annual berry production of rowan trees, (B) percentage of attacked berries by the apple fruit moth, and (C) percentage of parasitized larvae. Each line represents the time series from one study site.

variability among different locations. The moth population tracked the pattern in berry production (Fig. 3B, E), but the cyclicity was less pronounced than in berry production. This was particularly so in western Norway: the means of autocorrelations at lags 2, 3, 4, 7, and 8 were close to 0. For parasitoids, the results were more complex with large differences between locations (Fig. 3C, F). In western Norway (Fig. 3C), some locations indicated positive autocorrelations at lags of even numbers, but some showed positive autocorrelations at lags of odd numbers. It was difficult to detect any simple bottom-up signatures of the cyclic berry production at the parasitoid level.

Spatial synchrony

The berry production in rowan was synchronized among sites ($\bar{\rho} = 0.67$ with bootstrapped 95% confidence interval 0.63–0.70; Fig. 2A). The temporal fluctuation in abundance of the moth was also spatially synchronized ($\bar{\rho} = 0.43$ with bootstrapped 95% confidence interval 0.37–0.48, Fig. 2B). The degree of spatial synchrony in the parasitoid abundance was positive but lower than those in berry production and the moth ($\bar{\rho} = 0.30$ with

bootstrapped 95% confidence interval 0.23–0.37, Fig. 2C). Thus $\bar{\rho}$ decreased as trophic level increased.

The spatial correlation function (SCF) in berry production decreased with distance (Fig. 4A), showing that nearby trees are more synchronized than trees separated by greater distances. However, the decrease in synchrony was very shallow. Even across very large distances (> 300 km), reproduction was highly synchronized. SCFs of the infestation level by the moth and of the parasitism level of the moth larvae also indicated a smooth decrease in correlation with distance (Fig. 4B, C). However, the rate of decay became steeper with each trophic level. The SCF in berry production always exceeded that of the seed predator which in turn exceeded that of the parasitoids (though confidence intervals are partially overlapped).

Predator satiation

The log-proportion of healthy berries was negatively correlated with the amount of attacked berries in the previous year (partial Spearman's rank correlation (PSRC) = -0.35, Spearman's rank correlation (SRC) = -0.31; $p < 0.001$, Fig. 5A), but positively correlated with the amount of produced berries in the current year (PSRC = 0.53, SRC = 0.51, $p < 0.001$, Fig. 5A). We also observed a negative relationship between the seed predation and ratio in berry production (the slope = -0.50; SE = 0.03, Fig. 5B). The randomization test indicated that the slope of regression model was significantly negative at a nominal 10% level. Seed crops following poor seed crops thus tended to escape predations, implying a satiation through the predator's numerical response. If the numerical satiation of seed predators lasted for more than a year, we may find a negative relationship between the proportion of seed predated and the year-to-year ratio in berry production at greater time lags. Logistic regression analysis indicated a negative relationship between the two, however the randomization test revealed no evidence against the null hypothesis at the greater lags ($p > 0.1$). Significant numerical satiation of seed predators was only detected at a one-year lag.

Figure 6 shows the overall proportion of seeds attacked at each site as a function of the temporal variability in berry production, CV. The logistic regression revealed a significantly negative relationship between the proportion of berries predated and CV (the slope = -1.03; $p < 0.001$), indicating that the larger inter-annual variation in berry production resulted in the smaller loss to predation.

There were indications that the highest trophic level experienced satiation when its host was abundant. The log-proportion of healthy larvae was negatively correlated with the abundance of parasitoid larvae in the
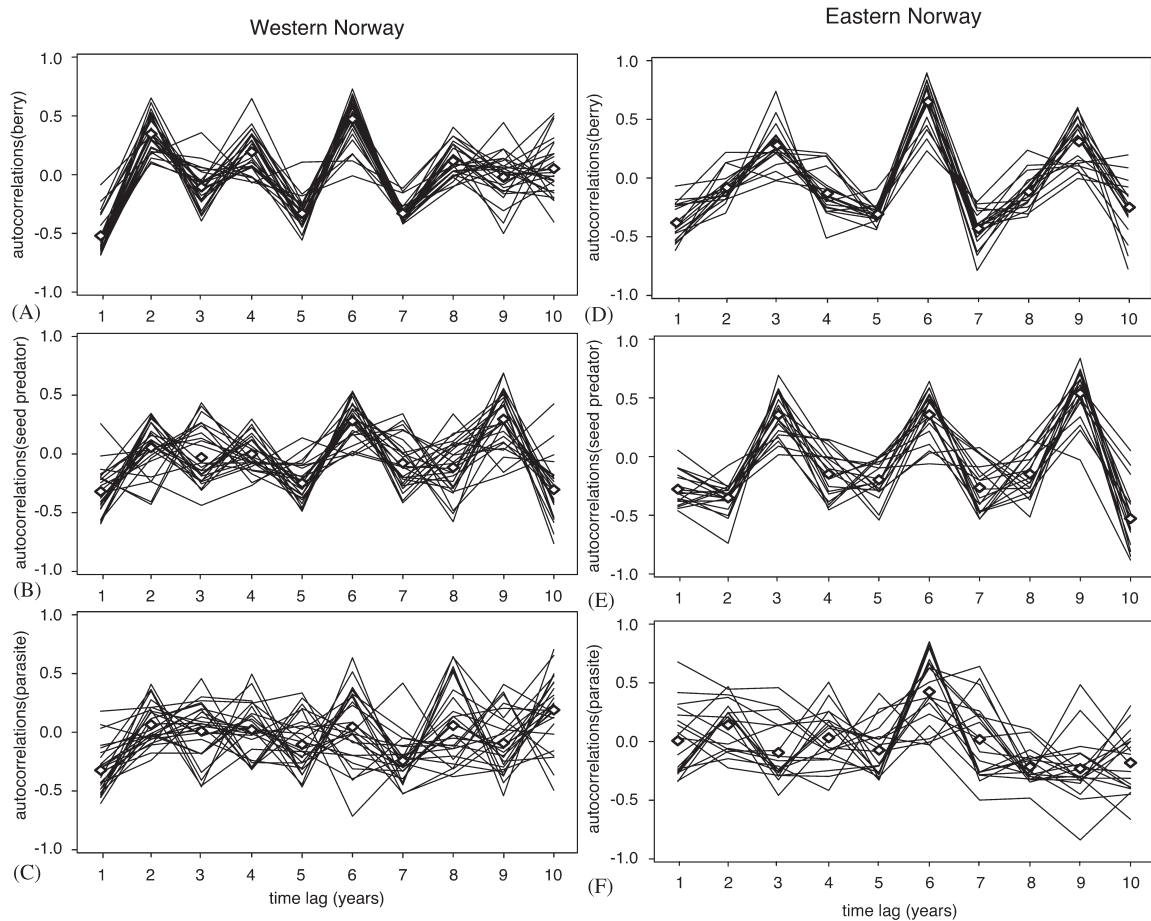
Fig. 3. Autocorrelation analysis of the time series data for each of the three trophic levels (rowan berries, apple fruit moths, and parasitoids). Results for western (26 sites, A–C) and in eastern (19 sites, D–F) Norway are plotted separately. Each line represents a different study site and diamonds indicate means over all sites.

previous year (PSRC = −0.45, SRC = −0.28; p < 0.001, Fig. 7A), but positively correlated with the abundance of larvae in the current year (PSRC = 0.53, SRC = 0.41, p < 0.001, Fig. 7A). Parasitism was also negatively correlated with the year-to-year ratio of host abundances (the slope = −0.39, SE = 0.07, Fig. 7B). This relationship, however, was not significantly negative in the randomization test, suggesting that the evidence of numerical satiation of the parasitoid was relatively weak.

Discussion

Berry production in rowan in southern Norway was variable across years and was spatially synchronized, testifying to conspicuous masting. The masting cycle in rowan was not fixed but exhibited geographically distinct patterns with a 2-year cycle in the west and a 3-year cycle in the east. This regional transition in fruiting dynamics may correlate with heterogeneous climatic conditions; western Norway is more oceanic and humid and may be

a better climatic region for trees to accumulate resources through an extended growing season (Søreide 2001). Geographical variations in dynamics induced by environmental heterogeneity and trophic interactions have been observed in a number of systems such as rodents (Saitoh et al. 1998), spruce budworms (Williams and Liebhold 2000), and Gypsy moth (Peltonen et al. 2002). We are currently exploring the effect of climatic conditions on determining the fruiting interval using a resource-based model for masting dynamics (Isagi et al. 1997, Satake and Iwasa 2000).

Large-scale spatial synchrony in berry production was observed (Fig. 4). There are two dominat hypotheses for the spatial synchrony of masting: pollen coupling (Isagi et al. 1997, Satake and Iwasa 2000, 2002a) and correlated environmental forcing (Koenig and Knops 1998, 2000, Koenig et al. 1999, Rees et al. 2002). At the large spatial scales in question, we conjecture that regionalized climatic forcing is likely to operate in addition to any pollen coupling. Distance-dependent processes, such as pollen exchange between nearby trees,
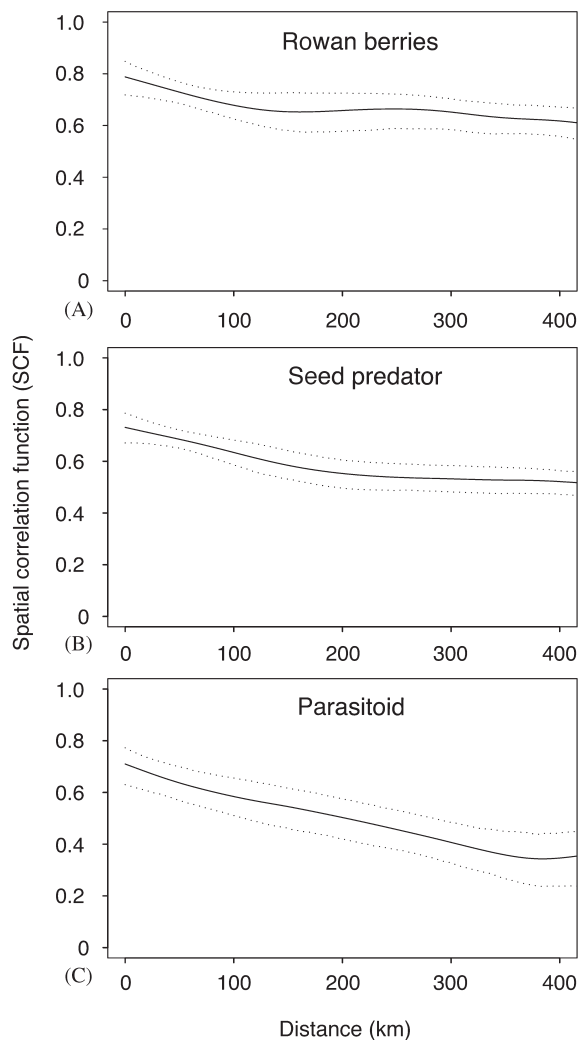
Fig. 4. Non-parametric spatial correlation functions (SCFs) of (A) berry production of rowan trees, (B) infestation level of apple fruit moth, and (C) level of parasitism. Solid lines represents SCFs and dashed lines are bootstrapped 95% confidence intervals. DF = 5.
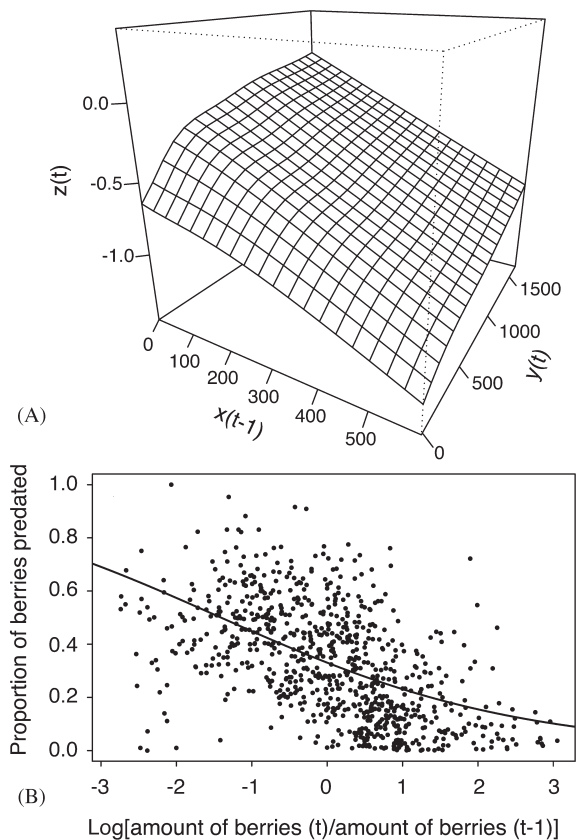

Fig. 5. The estimated function for the predator satiation. (A) The log-proportion of healthy berries, $z(t)$, as a function of the amount of berries predated in the previous year, $x(t-1)$, and the number of berries produced in the current year, $y(t)$. We estimate the function by using a two-dimentional smoothing spline (DF = 8). The function is statistically significant at a nominal 1% level. (B) The proportion of berries predated as a function of the ratio of number of berries produced in year t and that in year $t-1$ (lag1). Log transformed variables are used for calculation. Lines represents the logistic regression model which has intercepts and slopes of -0.73 (SE = 0.03, p < 0.001) and -0.50 (SE = 0.03, p < 0.001).

may induce synchrony at the local scale and external environmental forcing correlated at regional scales will work to strengthen and maintain such a synchrony between populations (Satake and Iwasa 2002b).

The rowan masting strongly influenced the dynamics at the higher trophic levels. The proportion of berries predated by the apple fruit moth varied across years and was synchronized between sites reflected by the masting dynamics. There were also influences on the highest trophic level-parasitism level of moth larvae fluctuated in a spatially synchronized fashion. The impact of masting on the highest trophic level appeared to be less pronounced as the tophic level goes up, as evidenced by decreased cyclicity (Fig. 3) and decreased spatial synchrony (Fig. 4). We speculate that this dampening in

cyclicity and synchrony through trophic interactions might be partially accounted for by the fact that the predator and the parasitoid are not strict specialists (the apple fruit moth switches the host to apple when the amount of rowan berries is very low). If predators and parasitoids are generalists who utilize multiple hosts, the dynamics of these species are affected not only by masting but also by dynamics of other hosts. In addition, if external environmental forcing that is independent of masting influences the population dynamics of the predator and parasitoid, the cascading effect of masting is likely to become less pronounced. There are at least three possible factors inducing spatial synchrony in predator/parasitoid populations: (1) migration, (2) geographically correlated environmental forcing, and (3) reflection of the synchrony in rowan berry production.
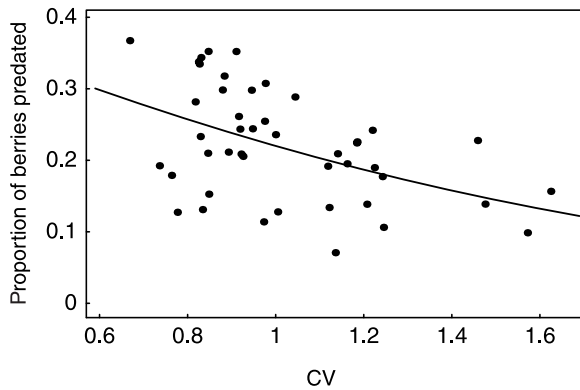
Fig. 6. Relationship between the coefficient of variation (CV) of annual seed production and the total proportion of seed predation. Each point represents the result calculated at a different study site. Logistic regression analysis gave the regression line with an intercept of -0.23 (SE = 0.29, p = 0.44) and a slope of -1.03 (SE = 0.29, p < 0.001).
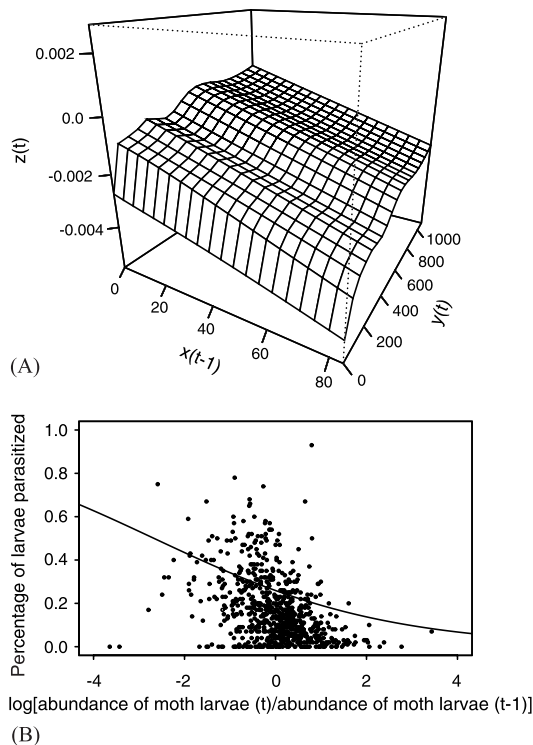

(A)

(B)

Fig. 7. The estimated function for the parasitoid satiation. (A) The log-proportion of healthy moth larvae, z(t), as a function of the abundance of moth larvae parasitized in the previous year, $x(t-1)$, and the abundance of moth larvae in the current year, y(t). We estimate the function by using a two-dimentional smoothing spline (DF = 9). The function is statistically significant at a nominal 1% level. (B) The proportion of moth larvae parasitized as a function of the ratio of abundance of larvae in year t and that in year $t-1$ (lag1). Log transformed variables are used for calculation. Lines show the logistic regression models which have intercepts and slopes of -1.05 (SE = 0.11, p < 0.001) and -0.39 (SE = 0.07, p < 0.001).

We speculate that migration is not important inducing spatial synchrony across the large geographic distances in question because the dispersal of the moth and the parasitoid presumably occur only in a very limited range. The geographically correlated environmental forcing and the reflection of rowan masting are likely to work in concert in our system. To assess the relative importance between the two in determining the population dynamics of the predator (or the parasitoid), we need to analyze how fluctuations in berry production and environmental forcing are correlated.

We attempted to assess two different components to the predator satiation, functional and numerical satiations, based on a simple population dynamics model (Eq. 1). The model predicts that functional satiations may be detected by testing for a positive relationship between the log-proportion of healthy berries and the amount of berries produced in the current year (Eq. 5). Numerical satiation, in contrast, can be detected by testing for a negative relationship between the log-scaled proportion of healthy berries and the amount of berries predated in the previous year (Eq. 5). These relationships were analyzed by using semiparametric model (Wood 2001), and partial correlations. The estimated relationships indicated that both of functional and numerical satiations are at work in our system (Fig. 5A). Another analysis to examine the satiation of seed predators showed a negative relationship between proportion of attacked berries and year-to-year ratio in berry production at lag 1 (Fig. 5B). Such a "ratio-dependent" pattern was previously documented by Kelly and Sullivan (1997) in their study of seed predation in *Chionochloa pallens*.

The more variable reproducers were more effective in escaping predation (Fig. 6), which is an important intraspecific test for the predator satiation hypothesis. Our analysis provides further evidence for predator satiation through the trophic chain: the response of parasitoids to fluctuations of their food resource was similar to those observed in the seed predator. The proportion of healthy larvae decreased with the abundance of moth larvae, but increases with the number of larvae parasitized (Fig. 7A). Furthermore the parasitism rate was negatively (albeit no significantly) correlated with the ratio in moth abundance (Fig. 7B).

These results provide strong supports for masting as a mechanism to reduce seed losses to predation, adding to how predation is a strong selective force on plant reproductive strategies (Janzen 1971, Silvertown 1980, Kelly and Sullivan 1997, Shibata et al. 1998, Kelly et al. 2000). Though rowan flowers are mainly pollinated by insects, for wind pollinated plants, masting is also beneficial by enhancing pollination success during synchronized above-average flowering effort (Nisson and Wästljung 1987, Norton and Kelly 1988, Smith et al. 1990, Kelly 1994, Kelly and Sullivan 1997). It is important to note, though, that in addition to the

advantages conveyed by masting, there are potential disadvantages associated with synchronized fluctuation in seed production – notably increased seedling competition (Kelly 1994) and lost opportunities for colonization or increasing risk of death (Waller 1979). The tension between these opposing forces will result in complex selective pressures on the reproductive schedules of individual plants. We believe that theoretical work combining the mechanism of energy allocation of plants and the dynamics of predator populations will be a next step in elucidating the selective benefits and the cascading consequences of masting.

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