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Phenology and abundance in relation to climatic variation in a sub-arctic insect herbivore–mountain birch system

Abstract The two forest-defoliating geometrid moth species *Operophtera brumata* and *Epirrita autumnata* are known to exhibit different altitudinal distribution patterns in northern birch forests. One possible explanation for this is that altitudinal climatic variation differentially affects the performance of two species through mismatching larval and host plant phenology. We explored this hypothesis by investigating the relationship between larval phenology and leaf phenology of *Betula pubescens*, which is the main host plant of both moth species, along ten replicate altitudinal transects during two springs with contrasting climate in northern Norway. There was a distinct monotonous cline in host plant phenology with increasing altitude in both years of the study, but the development of the leaves were generally 14 days later in the first of the 2 years due to cold spring weather. We found that larval development of both species closely tracked host plant leaf phenology independent of altitude and year. However, at the time of sampling, *E. autumnata* was approximately one instar ahead of *O. brumata* at all altitudes, probably reflecting that *E. autumnata* has faster early instar growth than *O. brumata*. The abundance of *O. brumata* was lowest at the altitudinal forest-line, while *E. autumnata* was lowest near sea level. Our results do not indicate that the altitudinal distribution patterns of the two moth species is due to any phenological mismatch between larval and host plant

phenology. We suggest rather that natural enemies at low altitudes limit larval survival and thus abundance of *E. autumnata*, while an early onset of winter at the forest limit reduces survival of late eclosing adults of *O. brumata*.

Introduction

Demonstrating how climate affects natural ecosystems is a challenge for scientists (Stenseth et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). A rapidly expanding literature shows that climate influences a variety of ecological processes. Examples are individual growth and development (Post and Stenseth 1999), phenology (Masters et al. 1998), and abundance (Parmesan et al. 1999; Thomas et al. 2004). Improved understanding of how climate affects ecological processes, and the mechanisms that are involved, would lead to better predictions of the impact of future climate change.

Herbivorous insects are functionally important in forest ecosystems, and concerns have been raised regarding how climate change may alter their impact on forest ecosystems (Niemelä et al. 2001). Northern birch forests support a rich fauna of herbivorous insects (Tenow 1963; Koponen 1973; Hågvar 1976; Koponen and Iso-Iivari 1978), some of which exhibit population outbreaks and consequently defoliate birch stands. The geometrid moth species *Epirrita autumnata* (autumnal moth) and *Operophtera brumata* (winter moth) are important defoliators of *Betula pubescens* (mountain birch) in Northern Fennoscandia. Both species show cyclic population dynamics with outbreaks occurring approximately every tenth year (Tenow 1972; Altenkirch 1991; Hogstad 1997). Such outbreaks can

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have dramatic and long-lasting effects on the forest (Nuorteva 1963; Kallio and Lehtonen 1973; Lehtonen and Heikkinen 1995; Tenow et al. 2001).

The role of climatic variation in geometrid moth outbreak dynamics in the mountain birch forests is not yet clear (Bylund 1999; Neuvonen et al. 1999). It is evident, however, that *O. brumata* and *E. autumnata* are climate sensitive, but somewhat differently. This is presumably reflected in the different distribution of geographic regions with outbreaking populations of the two species in Fennoscandia. While outbreaks of *E. autumnata* occur mainly in mature birch forests in sub-alpine areas in southern Scandinavia and in inland sub-arctic forests in northern Fennoscandia (Tenow and Bylund 1989; Ruohomäki et al. 1997), *O. brumata* outbreaks are usually restricted to warmer locations along the Norwegian coast or in inland south facing mountain slopes (Tenow 1972, 1996). Some of these differences are probably due to species-specific sensitivity to low winter temperatures, *O. brumata* eggs being somewhat more sensitive to low winter temperatures than *E. autumnata* (MacPhee 1967; Niemelä 1979; Tenow and Nilssen 1990). In birch forests bordering the Atlantic coast of Norway, however, minimum winter temperatures (−20°C) never even get close to lethal temperatures for either species. Still there is a distinct, greater small-scale differentiation in species-specific outbreak areas within these coastal forests which is related to altitude. *E. autumnata* outbreaks have been reported to predominate close to the tree-line, while *O. brumata* outbreaks are found at lower altitudes (Hågvar 1972; Tenow 1972; Hogstad 1997). Climate variation is often inferred to be the underlying cause for altitudinal distribution patterns in insects (Hodkinson and Bird 1998; Neuvonen et al. 1999).

Besides the direct effect of lethal winter temperatures, there are other aspects of climate that can affect the population dynamics of the two moth speciesmore indirectly. One such indirect influence may work through the phenology of the host plant (i.e. the mountain birch). Optimal conditions for the development of the moth larvae are achieved if they hatch in synchrony with budburst of their host plant. If hatching occurs before budburst, the larvae may starve to death, whereas late hatching implies reduced growth and survival since leaf quality drops rapidly with leaf maturation (Rockwood 1974; Feeny 1976; Ayres and MacLean 1987; Kaitaniemi et al. 1997; Van Dongen et al. 1997; Hunter and Elkinton 2000; Riipi et al. 2002). Consequently, it has been proposed that rapid climate change can cause a mismatch between larval hatching and budburst (Dewar and Watt 1992; Harrington et al. 1999; Visser and Holleman 2001). Moreover, the period with high-quality leaves may also become shorter if leaves develop more rapidly due to warmer climate (Junttila and Nilsen 1993), and this may affect the larvae adversely if they are not able to compensate with more rapid development. However, few systematic studies have investigated the extent to which spring feeding insects are capable of adjusting their development to spatial and temporal variability in climate and host plant phenology (Watt and McFarlane 2002). Also, few studies have been able to relate natural variation in phenology and climate to variation in abundance (Watt and Woiwod 1999).

Here we focus on larval development and abundance in sympatric populations of *O. brumata* and *E. autumnata* in relation to spatiotemporal variation in birch phenology in the coastal, sub-arctic birch forests in northern Norway. Because budburst in sub-arctic trees seems to be mainly determined by air temperature in the spring (Pop et al. 2000; Karlsson et al. 2003), we used altitude as the focal design variable in an observational study design. Air temperatures drop by 0.5°C to 0.65°C pr 100 m elevation under normal atmospheric pressure (Tveito et al. 2000), and so the leafing phenology of mountain birch can be expected to show a linear cline with altitude, providing that altitude is a reliable proxy of temperature change at the selected study site (Hodkinson and Bird 1998; Neuvonen et al. 1999). Beside altitudinal variation in temperature (and thus birch phenology), we included two contrasting years in terms of advancement of spring in this study. This made it possible to investigate the relative impacts of spatial and temporal components of climatic variation on larval phenology and abundance.

We address the following questions in this study:

- Does the phenology of sympatric *E. autumnata* and *O. brumata* populations match the phenology of birch in time and space, and do the two species differ in this respect?
- Does the abundance of larvae of the two moth species reflect larval/birch phenology and are there differences between the species?
- To what extent is it likely that climate determines the different distribution of altitudinal outbreak zones in the two species in coastal birch forests?

Materials and methods

Life cycle characteristics of the study species

The two study species, *E. autumnata* and *O. brumata*, have similar life cycles. The adults fly in the autumn, *E. autumnata* from mid August to mid September and *O. brumata* approximately 1 month later (Peterson and Nilssen 1998), whereas the eggs over-winter and hatch first in the following spring at leaf burst of their host plant. In northern Fennoscandia, the mountain birch *B. pubescens* is the most common and frequently used host for both species (Tenow 1972; Bylund 1999). The larvae go through five instars before they descend to the ground and pupate (Tenow 1972). Fully grown, the larvae of *E. autumnata* are about 20–27 mm long, and

the larvae of *O. brumata* are 15–22 mm. In both species, the duration of the larval stage is highly variable, just over 2–6 weeks in *E. autumnata* and 1–2 months in *O. brumata*, depending on temperature and forage quality (Tenow 1972; Ayres and MacLean 1987; Haukioja et al. 1988; Ruohomäki et al. 2000).

Description of the study area

The study was conducted at Reinøya in northern Norway (70°00′N, 19°49′E) during spring and early summer of 2001 and 2002. The climate is typically coastal subarctic with cool summers and relatively mild winters (Tveito et al. 2000). Figure 1 shows the daily mean temperatures for May, June and July as well as the cumulative temperature sums above the baseline of 0°C during the same period for the 2 years of the study. While spring and early summer were generally cooler than the average in 2001, the next year (2002) was warmer than normal.

The study area was located in a north-easterly oriented slope (mean slope 23.3°) where the forest forms a fairly homogenous belt from sea level up to a rather sharp forest limit at approximately 240–250 m elevation. The birch forest is a mosaic of heath and meadow type (Hämet-Ahti 1963), with scattered occurrence of rowan, *Sorbus aucuparia*, and willow, *Salix* spp. We established ten parallel altitudinal transects spaced at 200 m intervals from sea level to the forest limit. Each transect had four stations at the following altitudes: 30, 100, 170, and 240 m. The length of transects varied

Fig. 1 Daily mean temperatures and cumulative temperatures above 0°C after 1st May in 2001 and 2002 at the weather station of Tromsø, 40 km from the study site. Sampling dates for birch phenology and instar phenology are indicated by *small* and *large arrows*, respectively

between 514 m and 628 m. At each of the 40 transect stations, we measured 29 variables describing the forest structure and some other relevant environmental variables (see Appendix 1). A principal component analysis based on these measurements showed that the main feature of forest structure (PC1; Fig. 2) did not change monotonously with altitude. The forest consisted of open stands of relatively small birch trees both at the lowest and highest altitude, with denser stands composed of higher trees at the two intermediate altitudes. Mean snow depth, as indicated by height position of the lichen *Parmelia olivacea* on birch stems (Sonesson et al. 1994), increased with altitude (represented by PC2; Fig. 2).

Sampling and measurements

As a relative index of birch phenology we measured leaf size at three dates simultaneously at all 40 transect stations at the onset of the growing season. The first measurement date in each of the 2 years was selected such that leaves had not yet started to grow at the highest altitude. The first measurement date was May 29 in 2001 and May 15 in 2002, reflecting the difference in the onset of the growth season in the 2 years. Note also that the temperature sums were similar at the sampling date for the 2 years (Fig. 1). The subsequent two measurements were made approximately at weekly intervals. At each measurement date the size of nine undamaged leaves/buds from three different trees (i.e., 27 leaves in total) were measured at each sampling station (i.e. 270 leaves at each altitude). The size measurement was the length from the base to the tip of the bud/leaf with an accuracy of 1.0 mm.

Sampling of larvae for investigation of phenological development was conducted twice in June. As far as possible, ten larvae of each species were collected from the four sampling stations per altitudinal transect. The larvae were collected mainly by two methods: (1) shaking branches over a large plastic box and (2) sweeping a landing net through branches. Very small larvae may, however, not be sampled efficiently by these two methods, so the sampling was complemented by picking larvae from the leaves by hand during the first sampling occasion at the highest altitude (i.e. 240 m). To further minimize the sampling problem associated with small larvae, we chose the first sampling occasion so that larvae were at least in their second instar at all altitudes. Due to the different onset of the growth season in birch in the 2 years, the sampling occasions differed by 10 days in the 2 years. In 2001, the first sampling occasion was June 20 and 21, while the second occasion was June 27 and 28. In 2002, the equivalent days were June 10 and 11 and June 20 and 21, respectively. Again note that the temperature sums were similar at the sampling dates for the 2 years (Fig. 1). Because of time limitations, the eastern half of the altitudinal transects were sampled 1 day, whereas the western half was sampled the next day during each of the
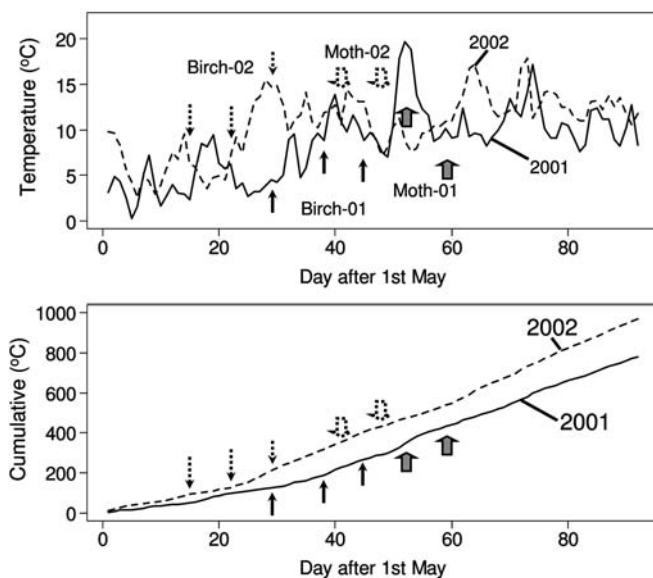
Axis 1

Axis 2

two sampling occasions. The larvae were frozen at −18°C until measurements were taken. In order to determine development stage (i.e. instars), head capsule width was measured under a magnifying lens with a measuring ocular and converted to millimeters. The width of the head capsule of the larvae was compared graphically to an empirical distribution smoothed using density estimation based on a non-parametric kernel to
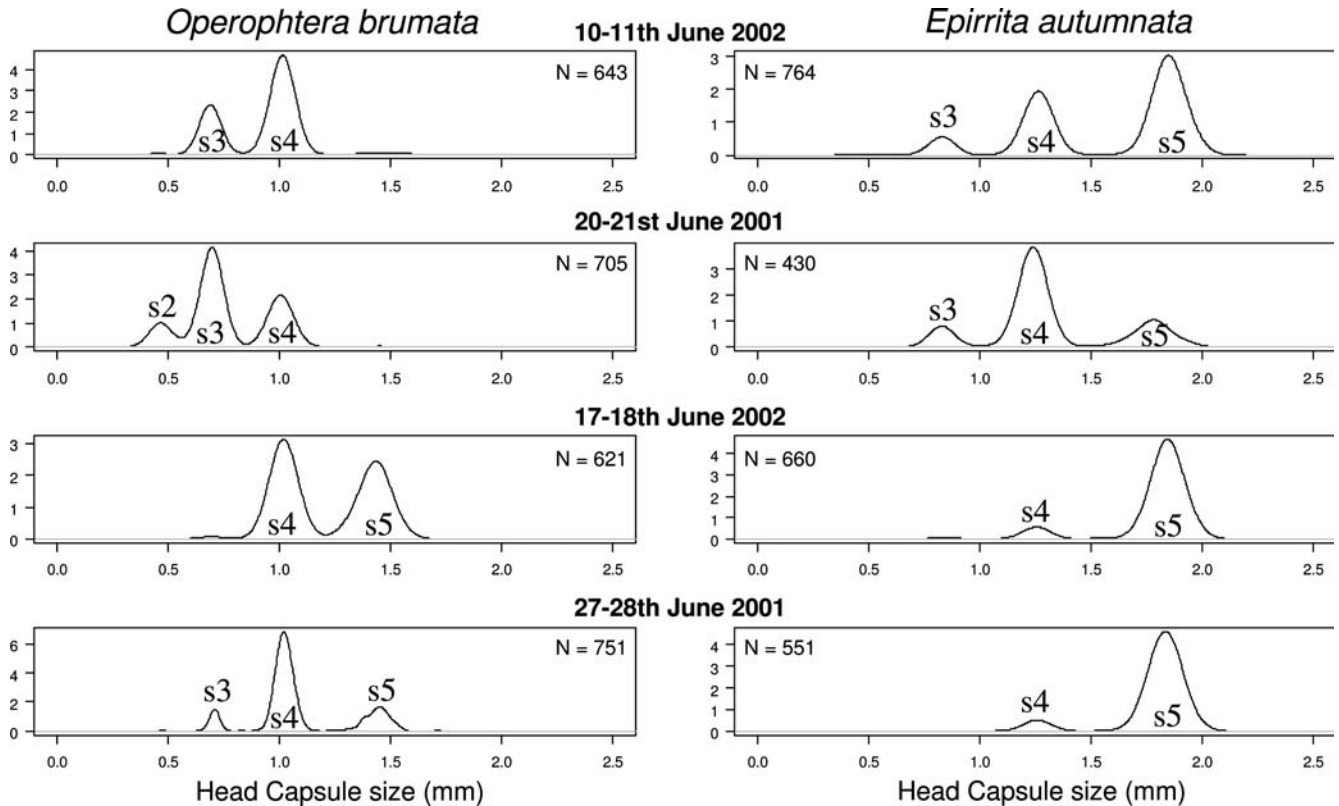

Fig. 3 Kernel estimates of frequency distribution of different instars (based on head capsule width) for the four samplings

separate the different instars (Fig. 3) (Venables and Ripley 1999). In the material, there were four instars (S2–S5) present for *O. brumata*, while only three instars (S3–S5) were present for *E. autumnata*. The limit values for head capsule width for instars 2–5 for *O. brumata* were respectively: 0.35–0.65, 0.65–0.90, 0.90–1.25 and 1.25–1.80 mm. For *E. autumnata* the limit values for instars 3–5 were respectively: 0.75–1.10, 1.10–1.50 and 1.50–2.13 mm.

The abundance of larvae was estimated at all transect stations on the first sampling occasion each year. This was done by counting the number of larvae on ten branches of an arm length size. Each branch was taken from a different tree within a radius of 50 m from the sampling station mark. The branch was carefully cut from the tree to avoid losing specimens, and thoroughly shaken in a large plastic box and the larvae counted.

Statistical methods

Abundance data (N) were analysed using a log transformation ($Log(N+1)$ since there were stations with $N=0$) and linear models. Predictor variables were year, altitude, the environmental variables as PCA scores on the two main axes (Fig. 2) or station specific values for snow level and tree height directly (i.e. the two main structuring variables). Polynomials were used to assess nonlinear relationships. Explained variation (R^2) and R^2 adjusted for numbers of parameters in the model (R^2_{adj}; it can be used to select models in a similar way to using AIC but has a more straightforward interpretation; Maindonald and Braun 2003) are given for the models fitted. Variability was assessed using standard deviation on the log scale, a measure of variability similar to a coefficient of variation. This measure of variability combines measurement error and true spatial variability, but as identical methods were used for all stations and given that the two moth species have similar biology, the comparison between years and altitudes is valid.

To compare larval development among the two species, different altitudes, years and dates within years, we focused on instar structure; i.e. the proportional distribution of different instars in altitude-specific larval samples. Models assuming a multinomial distribution and a logit link were used for this purpose. As very few larvae were observed in instar 2, and only on the first sampling, only instars three, four and five were considered. The model assumed that the two logits, $log(p4/p3)$ and $log(p5/p3)$ were linearly related to the predictor variables, and goodness of fit was assessed using the sum of squared Pearson's residuals for the two regressions (McCullagh and Nelder 1989). As the predictor variables, we included year, altitude and sampling data within the year and all possible interactions between them. Altitude was probed both as a categorical and as a continuous variable (in the latter case as a second order polynomial), whereas date was considered only a

categorical variable in the analysis. The model was 'fit' using the multinom-function in R (R Development Core Team 2004) and the model selection criteria BIC and AIC as well as the AIC and BIC weights were used to find the most appropriate models (Johnson and Omland 2004).

Results

Birch phenology

Phenology of birch, as indicated by the length measurements of buds/leaves in the two study years, is shown in Fig. 4. There was a distinct year difference in phenology, with the onset of growth in spring being approximately 14 days earlier in 2002 than in 2001. In both years, there were distinct monotonous clines in birch phenology with altitude. At the first measurement date, when buds had not burst yet at the highest altitude, the decrease in birch leaf/bud length was non-linear due to a bigger difference between the two lowest altitudes (i.e. 30 and 100 m) than between the subsequent intervals in altitude. However, the clines approached a linear relationship with time in both years; 2001 relatively faster than 2002.

Larval phenology

Multinomial modeling of instar structure showed that models with all main effects (altitude, year and sampling
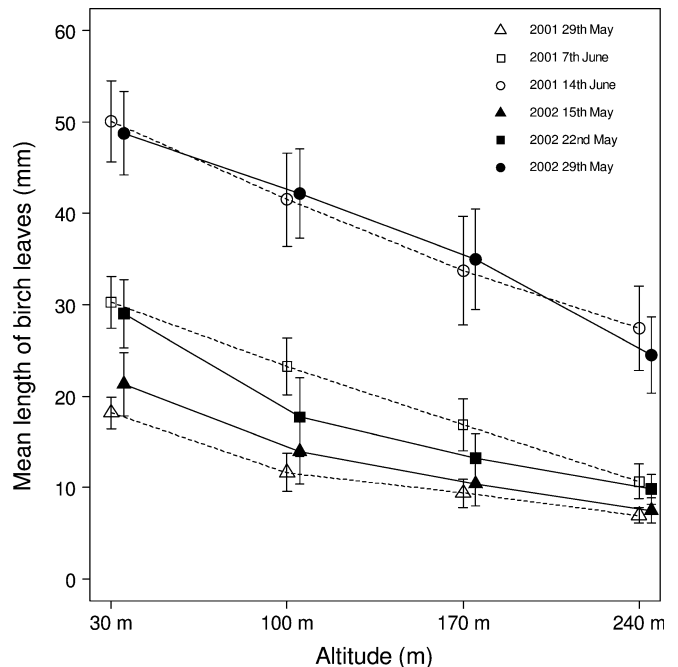

Fig. 4 Birch phenology shown as average length ($\pm$ SD) of the leaves at three dates in the altitudinal gradient

period) were needed for both species (Appendix 2). In addition, the most appropriate models according to the model selection criteria included the interactions sampling period × altitude and sampling period × year for *O. brumata*, while the interactions altitude × year and sampling period × year were included in the best model for *E. autumnata*. Although these interactions were included in the models, graphical representations of instar structure (Figs. 5, 6) revealed that strong main effects of altitude, year and sampling period dominated the instar structure of the two species.

At a given date there was a gradual shift towards earlier instars with increasing altitude, and this altitudinal change in instar structure appeared to be similar in both species and in both years (Figs. 5, 6). Figure 6 shows that the proportions of s4 and s5 for the first sampling period at 30 m and for second sampling period at 240 m were very similar, which means that for both species there was approximately a 1-week difference in larval development between the lowest (30 m) and highest (240 m) altitude. Within each year, the instar structure for *E. autumnata* was more advanced at any given date than that for *O. brumata*. The similarity between the instar structure for *O. brumata* in the second sampling period and *E. autumnata* for the first period (see Fig. 6) shows that *O. brumata* was lagging by approximately one instar and 1 week behind *E. autumnata* in both years (see also Figs. 3, 5). Even though the sampling period in 2002 was 10 days earlier than in

2001, the instar structure of both species was more advanced in 2002 than in 2001 (Figs. 3, 6), which indicates that the phenological difference between the 2 years was approximately 2 weeks.

The altitude × year interactions identified by the multinomial modeling for *E. autumnata* were mostly due to a larger difference in instar structure between 30 m and 100 m in 2001 than in 2002 (Fig. 6). The other interactions for both species is more difficult to discern, and is probably due to the fact that larval growth rates respond non-linearly to temperature depending on instar and time since molting (Ayres and MacLean 1987).

Larval abundance

There was much variation in abundance among sampling stations within altitudes in both species and years (Table 1). The variability was lower in 2002 than in 2001, particularly so for *E. autumnata* at the two higher altitudes (170 m and 240 m). Abundance of *O. brumata* was more variable than *E. autumnata* at nearly all altitudes and in both years. The most clear and consistent altitudinal pattern for abundance was that *O. brumata* was least abundant at the tree-line (240 m), while *E. autumnata* was least abundant at sea level (30 m; Fig. 7). A linear model including a year effect and a second-order polynomial for altitude explained 59% ($R^2_{adj} = 0.57$) of the variability of *E. autumnata*. The
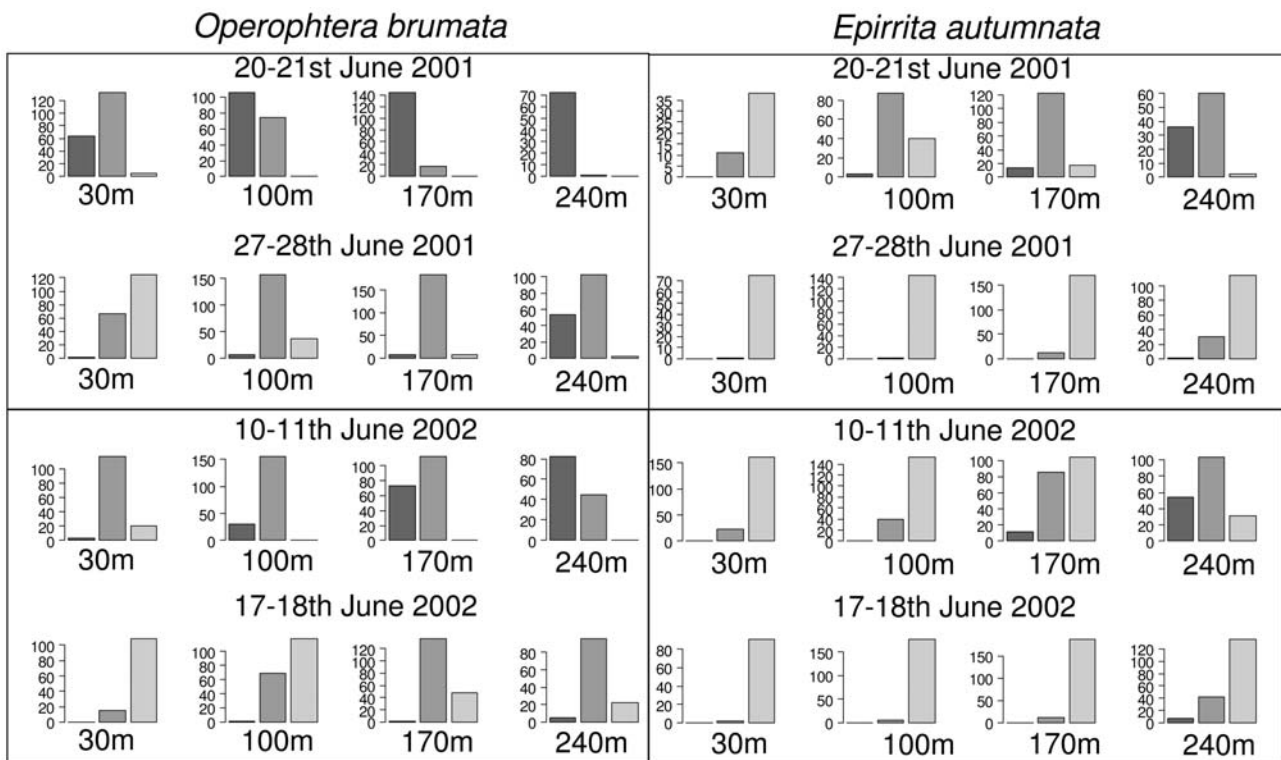

Fig. 5 Instar structure of *O. brumata* and *E. autumnata* depending on altitude, sampling period and year. *Y*-axis: number for larvae of an instar. *X*-axis: from *left* to *right* instar 3 (*dark shading*), instar 4 (*intermediate shading*) and instar 5 (*light shading*)
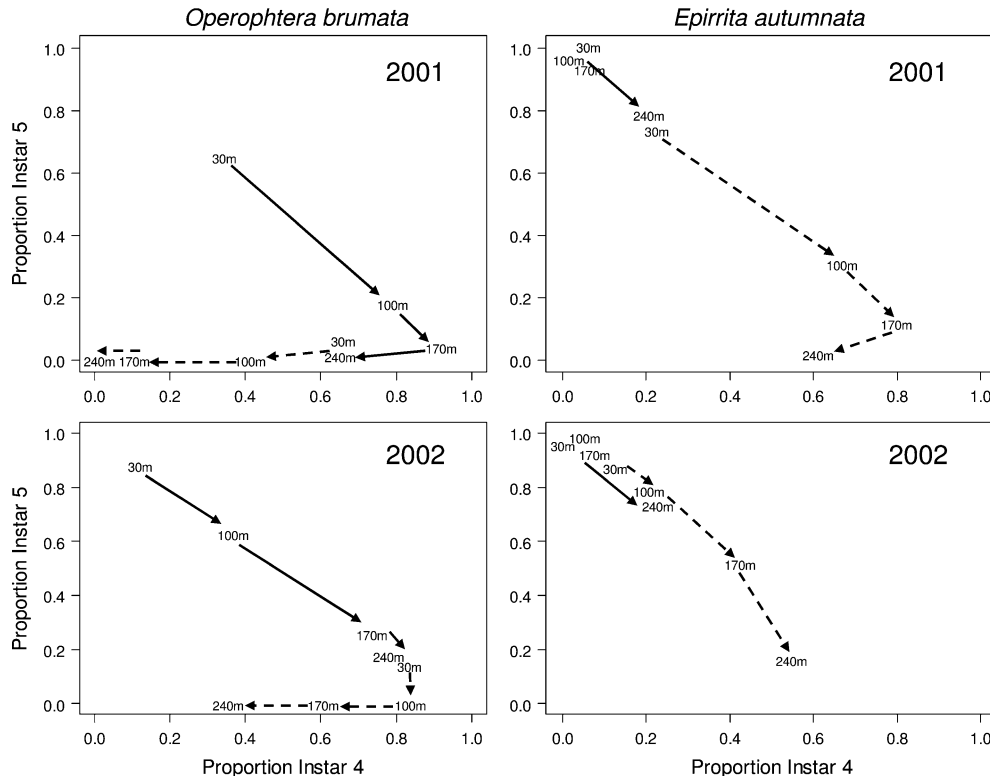
Fig. 6 Change in instar structure with altitude at given dates for *O. brumata* and *E. autumnata* in 2001 and 2002. Instar structure (denoted by the sampling altitude) is expressed as the proportion instar 4 and 5 of all three instars (s3 + s4 + s5). The *arrows* connect the proportions at increasing altitudes for the same sampling period. *Broken arrows*: first sampling period in a year (20–21 June in 2001, 10–11 June in 2002). *Whole arrows*: second sampling period in a year (27–28 June in 2001, 17–18 June in 2002)

Table 1 Abundance of *Epirrita autumnata* and *Operophtera brumata* in relation to altitude and year

O. brumata (m)	2001	2002	*E. autumnata* (m)	2001	2002
30	2.77 (0.83)	1.60 (0.99)	30	0.61 (0.45)	1.09 (0.52)
100	2.66 (0.93)	2.50 (0.63)	100	1.77 (0.47)	2.46 (0.53)
170	2.70 (1.36)	2.53 (0.71)	170	1.89 (0.81)	2.99 (0.43)
240	1.44 (0.79)	1.52 (0.73)	240	1.38 (0.95)	2.22 (0.55)

Mean $\log(N+1)$ with standard deviations in parenthesis. Standard deviation on a log scale is analogous to a coefficient of variation on the original scale

highest abundances were observed at the intermediate altitudes, as shown by the coefficients of a second order polynomial [alt: 0.031 (SE = 0.0039); alt^2: −0.000098 (SE = 0.000014)]. *E. autumnata* increased in abundance from 2001 to 2002 [coefficient: 0.779 (SE = 0.137)]. The same model for *O. brumata* explained only 23% (R^2_{adj} = 0.20) of the variability. The abundance of *O. brumata* were also highest at intermediate altitudes [Fig. 5; alt: 0.018 (SE = 0.0058); alt^2: −0.000078 (SE = 0.000021)], but there was no strong evidence for an increase or decrease in abundance between 2001 and 2002 [−0.358 (SE = 0.204)]. Models including year and either second order polynomials of the first two PCA axes (*E. autumnata* R^2 = 0.38, R^2_{adj} = 0.33, Δ AIC = 37.3; *O. brumata* R^2 = 0.20; R^2_{adj} = 0.15, Δ AIC = 6.31) or of snow level and tree height (*E. autumnata* R^2 = 0.29;

R^2_{adj} = 0.25, Δ AIC = 6.17; *O. brumata* R^2 = 0.20; R^2_{adj} = 0.15, Δ AIC = 5.58) explained less than models including altitude (and did not explain additional variability when altitude was included in the model: year + alt + alt^2 + Axis 1 + (Axis 1)^2 + Axis 2 + (Axis 2)^2: *E. autumnata* R^2 = 0.61, R^2_{adj} = 0.55, Δ AIC = 4.57; *O. brumata* R^2 = 0.25; R^2_{adj} = 0.17, Δ AIC = 4.96). The latter indicated that vegetation structure did not explain the spatial variability within altitudes.

Discussion

The timing of hatching of larvae from eggs in many spring feeding insects is often determined by simple rules

Fig. 7 Abundance distribution of *O. brumata* and *E. autumnata* in the altitudinal gradient in the 2 years of this study. The box plots are based on number of larvae per sampling station. There are ten sampling stations per altitude
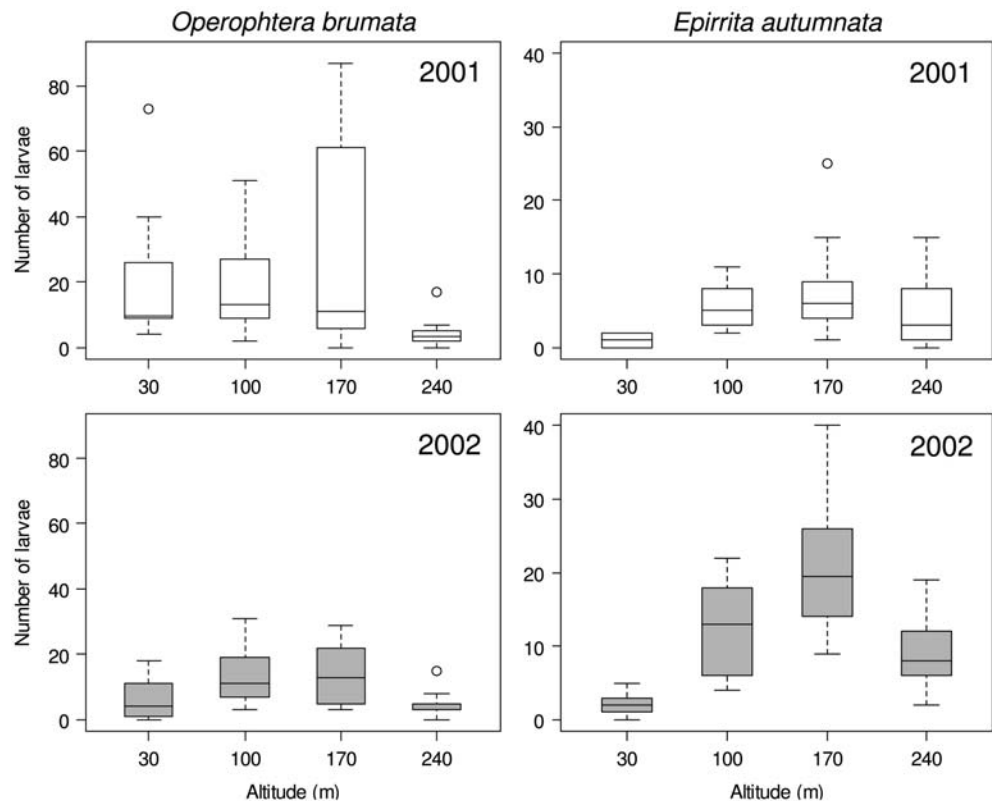
based on temperatures during spring (but see Kaitaniemi and Ruohomäki 1999). Climate can interfere directly with larval development rates in several ways. In central Europe, 50% of *O. brumata* hatched when the number of degree-days, i.e. the sum of temperatures over 3.9°C, varied from 200 to 380 depending on the number of frost days (Visser and Holleman 2001). The hatching rule for *E. autumnata* was that 50% of the eggs hatched when the number of degree-days above a threshold of 5.8°C was 262 in December, and in February the corresponding figures were 362 and −2°C (Nilssen and Tenow 1990). Whatever the species-specific hatching rules are, it is important that match the budburst of the host plants, as mismatch can result in non-optimal growth conditions for the larvae (Ayres and MacLean 1987; Visser and Holleman 2001).

Our monitoring of the development of birch leaves and moth larvae suggests that the phenology of both the plant and insect herbivores respond very similarly to altitude and the contrasting climate during the 2 years. Both in birch and moths there was approximately a 1-week difference in phenology between the lowest and highest altitude. Moreover, in year 2002, the development of the studied plant–herbivore system was approximate 14 days earlier than in 2001. Thus, the two moth species seemed to be able to match their development with that of their host plant in time and space. Consistent with this finding, a study on *O. brumata* and oak (*Quercus robur*) showed that *O. brumata* larvae was able to hatch in synchrony with bud burst of its host when spring temperature was experimentally elevated in

controlled setting (Buse and Good 1996). However, in yet another study, *O. brumata* did not appear to always match the phenology of Sitka spruce (*Picea sitchensis*) (Dewar and Watt 1992). Watt and McFarlane (2002) argued that there was a strong need for studies comparing phenology of spring feeding insects and their hosts under natural conditions.

One of the most interesting findings in our study was the very clear and consistent difference between the two moth species. Even though both species are known to synchronize their hatching with bud burst (Ayres and MacLean 1987; Ruohomäki et al. 1997; Visser and Holleman 2001), *E. autumnata* finished its larval period faster than *O. brumata*. Specifically, *E. autumnata* was approximately one instar and 1 week ahead of *O. brumata* at all altitudes and sampling dates. Also Hågvar (1972) found that *E. autumnata* was in a more advanced stage of development than *O. brumata* in an altitudinal gradient in south Norway. If both species indeed follow the same hatching rule (see above), *E. autumnata* must grow faster than *O. brumata* at earlier instars than were monitored in this study (i.e. s1 and s2). Proximately this may be due to the fact that *E. autumnata* has relatively much larger eggs than *O. brumata* (Tenow 1972), and therefore has more resources when starting to grow. Another possibility is that *E. autumnata* grows faster at low temperatures. However, the latter explanation does not fit the fact that the phenological difference between the species was largely unaffected by altitude (and thus temperature) in this study. A third possible explanation for a higher

early growth in *E. autumnata* is stage specific feeding strategy. Larvae of *E. autumnata* in all stages feeds freely on leaves, while early instar *O. brumata* (s1 and s2) forage between leaves spun together (Tenow 1972). This cryptic feeding strategy in early instars of *O. brumata* may incur costs in terms of reduced feeding efficiency and consequently slower early growth. Regardless of the proximate mechanism, a shorter development time for *E. autumnata* than *O. brumata* could have evolved to achieve an early eclosion in the fall, in environments which have an early onset of winter (see below).

A main question motivating the present study was whether altitudinal climatic variation in larval phenology can contribute to the explanation of the large-scale distribution pattern of *O. brumata* and *E. autumnata*. The distribution ranges of the two moth species are largely overlapping, but differ in some important aspects. The outbreaks of *E. autumnata* occur mainly in mature inland forests (Tenow and Bylund 1989; Ruohomäki et al. 1997), whereas the outbreak of *O. brumata* are restricted to warmer locations along the Norwegian coast and inland south facing mountain slopes. A reason for this large-scale pattern (inland–coast) has been suggested to be due to differences in egg cold hardiness between the species, preventing *O. brumata* from colonizing the coldest inland areas (MacPhee 1967; Niemelä 1979). The lowest winter temperature measured in Tromsø since 1920 is −18.4°C (P.T. Sørvoll, Meterological institute in Tromsø, personal communications). This minimum is far above the super cooling point for the eggs of the most vulnerable species; i.e. −35°C for *O. brumata* (MacPhee 1967). Where the two moth species occur together, *E. autumnata* has been found to be most abundant in the upper part of the birch forest, while the main distribution of *O. brumata* is shifted towards the middle and lower parts (Tenow 1972, 1996; Hågvar 1976). The abundance distribution of the two species in the altitudinal gradient of the present study mainly conforms to these earlier findings. The main drop in abundance of *E. autumnata* was found at the lowest altitude, while the abundance of *O. brumata* was lowest at the highest altitude. With respect to the possibility that phenological problems faced by the larvae (e.g. due to a developmental mismatch between plant and insect) could be responsible for these altitudinal patterns in the abundance distributions, the present study does not offer much support. In particular, *E. autumnata* seemed to grow well and fulfil its life cycle normally even at the lowest altitude. Neither was there anything exceptional with the development rate in *O. brumata* at the highest altitude. Thus, one may suspect that causes other than larval phenology were more important for the distribution pattern.

One of the biggest differences in the life history of the two species is the timing of eclosion from pupae in the fall. The main period for eclosion of *E. autumnata* is from mid August until mid September (Peterson and Nilssen 1996), while the corresponding period for *O. brumata* is 1 month later (Peterson and Nilssen 1998). The most favoured explanation for the late eclosion in *O. brumata* is that it may be a strategy for avoidance of predatory beetles such as Staphylinidae (Topp 1979) and Carabidae (Thiele 1969; Trittelvitz and Topp 1980), that could easily prey on the flightless female. Since these predators become inactive later in the fall, it may pay off for the moth to postpone its eclosion. Other authors have hypothesized that predation by birds determine the eclosion time. For *E. autumnata* predation by passerine birds was as high as 20–30% in August, but decreased markedly throughout September (Tammaru et al. 1996, see also Tammaru et al. 2001). The most important avian predators, such as *Muscicapa hypoleuca*, *Phylloscopus trochilus*, *Anthus trivialis* and *Motacilla alba*, normally migrate south in the beginning of September, and by September 15 none of these species is present in our study area (Strann and Nilssen 1997). Consequently, when *O. brumata* emerges in late September, the most specialized insect predators among the birds are absent (Peterson and Nilssen 1998). Whereas predation on the adult moths imposes a strong and direct selection pressure for late adult eclosion, early snowfall has the opposite effect in terms of high mortality for those individuals that have not yet emerged from the ground. Such early snowfall happens more frequently at high altitudes, and indeed disruption of emergence by early snowfall in *O. brumata* has been observed at high-altitude sites in Scotland (Kerslake et al. 1996). Thus it seems reasonable to suggest that the timing of eclosion of the two species represents two different strategies. The late eclosion of *O. brumata* is mainly a strategy against a rich fauna of generalist predators at low latitudes, while the earlier eclosion of *E. autumnata* is supposed to lower the risk of adults being trapped in snow at higher altitudes where the fauna of predators is poorer (Hågvar 1976). A natural consequence of these two strategies is that *E. autumnata* would become less abundant at low altitudes because of predators, while *O. brumata* would become less abundant at high altitudes because of early snowfall. Local adaptation over the short distance in steep altitudinal gradients will probably not be possible because of extensive gene flow.

Conclusion

Two major insect defoliators of birch in coastal, subarctic forest—the autumnal moth *E. autumnata* and the winter moth *O. brumata*—appeared to able to match their phenology adequately to that of their host plant along a altitudinal gradient from sea level to the mountain forest limit, in two contrasting years in terms of the onset of spring. Although one of the moth species (*O. brumata*) completed its larval stage about 1 week later than the other (*E. autumnata*) this could hardly explain the different altitudinal distribution patterns of

the two species since they responded very similarly to changes in altitude in terms of larval development. Other climate-related mechanisms, such as predation by generalist predators during the larval and adult stage in *E. autumnata* at low altitude, and failed eclosion due to early snowfall at high altitude in *O. brumata*, seem to be better candidates for explaining the different altitudinal outbreak ranges of the two species.

Appendices for electronic archive

Appendix 1

At all transects stations a 50 m long sampling line was drawn horizontally on each side of the station. Vegetation cover variables for dominating species of the tree-, shrub- and field layers, and occurrence of streams and boulders was recorded at each meter along the sampling lines (see Table 2 for a description of variables). Additionally, at each station and at the two ends of the sampling line stand density, canopy height, snow depth and slope were recorded. Long-term average snow depth was measured by the mean height position of the lichen *Parmelia olivacea* on birch stems (Sonesson et al. 1994).

In the PCA of forest characteristics, two principal components, PC1 and PC2, accounted for 44.3% of the variance between sampling stations (Fig. 8). PC1 was mainly associated with tree height and accounted for 29.3%, while PC2 was associated with snow level and accounted for 15.0%. Tree height was positively correlated with tree density, presence of deadwood, high perennials and litter, and negatively correlated with presence of bushes and moss in mats. Snow level was positively correlated with slope and presence of blueberry, and negatively correlated with peat moss, moss in tufts, heather and grass.

Table 2 Codes and description for variables used to characterize the forest along the altitudinal transects

Code	Description
Tree < 2 m b	*Betula pubescens* under 2 m
Tree 2–4 b	*B. pubescens* between 2 m and 4 m
Tree > 4 m b	*B. pubescens* over 4 m
Tree < 2 m s	*Salix caprea* under 2 m
Tree 2–4 s	*S. caprea* between 2 m and 4 m
Tree > 4 m s	*S. caprea* over 4 m
Tree < 2 m r	*Sorbus aucuparia* under 2 m
Tree 2–4 r	*S. aucuparia* between 2 m and 4 m
Tree > 4 m r	*S. aucuparia* over 4 m
Bush e	Bush layer dominated by *Juniperus communis*
Bush sa	Bush layer dominated by *Salix* spp
Bush d	Bush layer dominated by *Betula* nana
Field hu	Field layer dominated by high perennial herbs
Field lu	Field layer dominated by low perennial herbs
Field gr	Field layer dominated by grass
Field l	Field layer dominated by heather
Ground la	Ground layer dominated by lichen
Ground mm	Ground layer dominated by moss in mats
Ground to	Ground layer dominated by peat moss
Ground tm	Ground layer dominated by moss in tufts
Ground st	Ground layer dominated by litter
Ground se	Ground layer dominated by stone
Ground be	Ground layer dominated by creek
Deadwood	Deadwood present on the sampling line
Billberry	Billberry *Vaccinium myrtillus* present on the sampling line
Tree density	Density of trees measured at each station at 50 m from the station at each side at the same altitude
Tree height	Mean height of the five tallest trees at each station and at 50 m from the station at each side at the same altitude
Slope	Slope measured at each station and at 50 m from the station at each side at the same altitude
Snowlevel	Mean height of the lichen *Parmelia olivacea* of 15 trees at each station

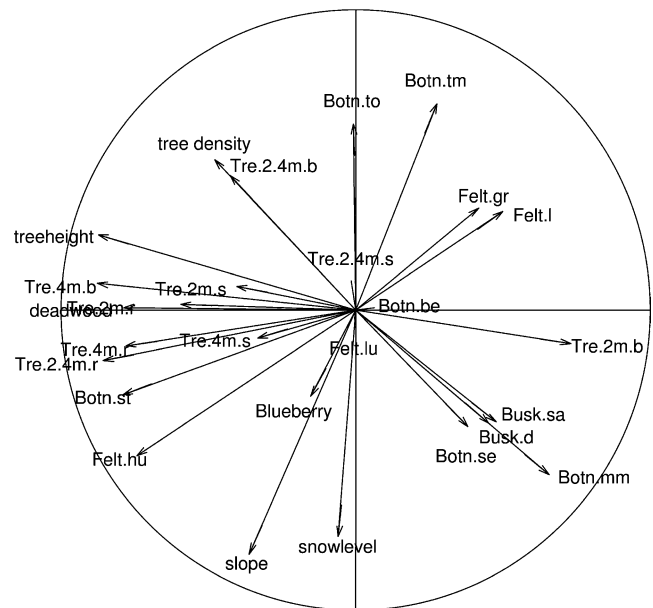**Fig. 8** The association between the original forest characteristics variables and the two first principal components derived from the PCA. For description of variables see Table 2. The *unit circle* indicates the maximum correlation that could be observed between each of the PC and the original variables. The *variables with arrows close to the circle* are very well explained by the first two PC axes

Appendix 2

Results of the multinomial modelling of instar structure, where the different models are ranked according to the two model selection criteria Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC). The models with the strongest support according to AIC/BIC weights are considered to be the most appropriate (i.e. the models in bold for both species). Terms included in different models are indicated with a X. Alt_q: altitude as a continuous variable; Alt_P2: second order polynomial for Alt_q; Alt_c: Altitude as a categorical variable. Np Number of parameters. The model Date: (Alt_q + Year) fitted both $O.brumata$ (Pearson's chi square = 19.39, df = 23, P = 0.68) and $E.\ autumnata$ (Person's chi square = 28.95, df = 23, P = 0.18; excluding one observation with a very large residual, but not affecting model parameters estimates)

Species	Alt_q	Alt_P2	Alt_c	Date	Year	AltP2:Year	AltP2:Date	Alt_c:Year	Alt_c:Date	Date:Year	Date:Year:Alt_c	Np	AICc	BIC	AIC weigths	BIC weights
O. brumata	X	X		X	X		X					**26**	**0**	**0**	**0.32**	**0.84**
	X	X		X	X							14	21.78	4.2	0.00	0.10
	X	X		X	X	X						30	1.48	7.3	0.15	0.02
	X	X		X	X	X	X					**32**	**-0.82**	**8.0**	**0.48**	**0.02**
			X	X	X				X			22	14.05	8.2	0.00	0.01
			X	X	X							16	24.99	10.3	0.00	0.00
	X		X	X	X			X				28	12.02	15.0	0.01	0.00
			X	X	X			X				34	6.99	18.7	0.00	0.00
			X	X	X				X			12	39.42	18.9	0.00	0.00
			X	X	X			X	X			22	26.74	20.9	0.01	0.00
			X	X	X			X	X			40	6.6	27.1	0.01	0.00
			X	X	X			X	X			40	10.78	31.3	0.00	0.00
			X	X	X			X	X			46	4.39	33.7	0.04	0.00
			X	X	X			X	X	X	X	64	19.67	75.4	0.00	0.00
E. autumnata			X	X	X			X		X		**28**	**0**	**0**	**0.99**	**0.53**
			X	X	X			X				**22**	**9**	**0.2**	**0.01**	**0.47**
	X		X	X	X			X		X		32	19.54	25.4	0.00	0.00
	X		X	X	X			X				22	36.99	28.2	0.00	0.00
			X	X	X		X		X			46	21.53	47.9	0.00	0.00
			X	X	X		X		X			40	33.16	50.7	0.00	0.00
	X		X	X	X							12	89.89	66.4	0.00	0.00
	X		X	X	X							14	92.15	71.6	0.00	0.00
			X	X	X				X			16	92.52	74.9	0.00	0.00
	X		X	X	X				X			30	76.34	79.3	0.00	0.00
	X		X	X	X		X		X		X	64	36.99	89.8	0.00	0.00
	X		X	X	X		X		X			26	106.58	103.6	0.00	0.00
	X		X	X	X				X			40	94.18	111.8	0.00	0.00
			X	X	X				X			34	119.13	127.9	0.00	0.00

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