Multi-objective optimization shapes ecological variation

Pekka Kaitaniemi[1], Annette Scheiner[2], Tero Klemola[2], Kai Ruohomäki[2]

[1]Hyytiälä Forestry Field Station, Department of Forest Sciences, University of Helsinki, Hyytiäläntie 124, 35500 Korkeakoski, Finland
[2]Section of Ecology, Department of Biology, University of Turku, 20014 Turku, Finland

Ecological systems contain a huge amount of quantitative variation between and within species and locations, which makes it difficult to obtain unambiguous verification of theoretical predictions. Ordinary experiments consider just a few explanatory factors and are prone to providing oversimplified answers because they ignore the complexity of the factors that underlie variation. We used multi-objective optimization (MO) for a mechanistic analysis of the potential ecological and evolutionary causes and consequences of variation in the life-history traits of a species of moth. Optimal life-history solutions were sought for environmental conditions where different life stages of the moth were subject to predation and other known fitness-reducing factors in a manner that was dependent on the duration of these life stages and on variable mortality rates. We found that multi-objective optimal solutions to these conditions that the moths regularly experience explained most of the life-history variation within this species. Our results demonstrate that variation can have a causal interpretation even for organisms under steady conditions. The results suggest that weather and species interactions can act as underlying causes of variation, and MO acts as a corresponding adaptive mechanism that maintains variation in the traits of organisms.

Keywords: computational ecology; life history; optimization; variation

INTRODUCTION

Characteristic of ecological thinking is the attempt to identify and classify different forms of ecological strategies that describe regularities in the ways organisms collect and use resources in their environment in order to maximize their fitness. Typically, there are multiple strategies for coping with the same environmental factors, and these alternatives are presented in terms of phenotypic trade-offs. A lot of theory has been built around the existing alternative strategies and trade-offs, for example, between size and number, honesty and cheating, growth and defence, and producing male or female offspring [1,2]. Trade-offs can take place at many levels of organization ranging

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from low-level choices between physiological pathways [3] to high-level traits such as alternative timings of life-history events [4].

In order to reach maximum fitness, organisms can adjust their innate phenotypic strategy through phenotypic plasticity [5]. The trading off of phenotypic traits is assumed to take place through finding an optimal solution to the developmental decisions modifying phenotype [5]. As organisms interact with their local environment, it is possible to identify a large number of potential factors that produce trade-off decisions and fitness consequences requiring plastic responses to cope with the environment. Growth rate, for example, is a central component of fitness in many organisms and requires phenotypic adjustment owing to trading off between the costs and advantages of growing rapidly. These costs and advantages may result, for example, from time constraints in a seasonal environment, from predator-dependent or predator-independent mortality, from limited food availability, or from the need to optimize other essential physiological functions in addition to growth rate [6].

Experiments usually consider just a few phenotypic factors and hence are prone to providing oversimplified implications for many theoretical considerations because they ignore the full complexity of the environmental factors that underlie variation in the phenotype [7]. For example, it is well known that weather factors modify the outcome of experiments, and they may even shape the genetic composition of populations [8], yet it is rare for experiments to systematically include different weather alternatives. Accordingly, experimental results in ecology usually contain a huge amount of quantitative phenotypic variation among and within species and locations, which often makes the theoretical interpretation of many experimental results difficult. Experimental simplifications work best when the formation of a specific phenotype is investigated in a spatially and temporally restricted ecological system and under the influence of just some specific factors. However, interpreting the complexity and variation of ecological systems in a generalizable and theoretically plausible way requires direct consideration of the complex implications of the variation present between and within species and locations.

It is well known that alternative phenotypic traits may provide organisms with equal fitness. In game theoretical settings [2], for example, a typical game predicts players who achieve equal fitness with clearly distinctive phenotypic strategies. In actual ecological systems, there are more than two or three phenotypic traits and environmental factors that contribute to an organism's final fitness. For example, the final fitness of an insect might depend on egg size and number, and on the oviposition sites of eggs, as well as on all other insect traits that contribute to them.

Multi-objective optimization (MO) is a method for solving problems that optimizes a large number of objectives (such as a set of phenotypic traits contributing

to an insect's fitness) and that simultaneously involves trade-offs among the alternative objectives [9]. MO is essentially an extension of traditional optimization models, which concentrate on optimization of decisions concerning only single traits. For example, single-trait optimization might investigate the timing of metamorphosis in the life history of an organism [4] without considering the potential fitness consequences of other life events, such as the timing of oviposition. An MO problem, in turn, could include a search space of alternative timings for all life stages, with the timings being expressed in terms of their fitness consequences. MO could then be used to find the best set of timings for maximizing fitness, thereby forming an optimal lifetime phenotypic life-history strategy.

The logic of MO somewhat resembles game theory, and MO can be thought of as a multi-dimensional game with continuous strategies. Similar to game theory [2], different combinations of phenotypic traits can produce alternative but equally optimal solutions to maximize fitness. This also distinguishes MO from classical optimization, where a single global optimum is commonly assumed and sought. An MO problem may involve an unfixed number of environmental factors that act as 'opponents' and a player with a strategy based on a suite of continuous phenotypic traits. The payoffs from the player phenotype are then determined by the fitness consequences of interactions among the phenotype and the environment where the phenotype occurs.

In engineering and economics, MO is frequently used for optimizing resource allocation [9]. However, MO appears in the ecological and evolutionary literature rather infrequently, and examples that develop the theory beyond plain parameter estimation are limited to studies of the behavioural strategies of animals [10,11] and variation in plant form and function [12,13]. Here, we suggest that MO provides a general analytical method for inferring the causes and consequences of the variation that characterizes individual organisms and the resultant species assemblages. As an example, we will consider variation observed experimentally in the life-history traits of an insect, and we will show that MO provides a logical causal explanation for previously unexplained 'random' variation even in this simplified single-species system.

MATERIALS AND METHODS

(a) Study species

As an example of an MO problem, we considered the fitness consequences of life-history traits in females of the autumnal moth *Epirrita autumnata* (Bkh.; Lepidoptera, Geometridae). *Epirrita autumnata* is a species of moth that has a 9–10 year population cycle producing periodic population outbreaks in northern Fennoscandia, resulting in severe defoliations of mountain birch (*Betula pubescens* ssp. *czerepanovii* Orlova;

Hämet-Ahti) forests [14]. It overwinters in the egg stage; the larvae hatch around the time of budbreak in the mountain birch, after which they feed for about four to six weeks. The subsequent pupal period takes six or more weeks, after which the adults emerge and the females lay their eggs after mating [15]. The different life stages of *E. autumnata* are the target of a well-documented group of predators and parasitoids that have long been the subject of intense study in different population phases [16]. In addition, the food-related fitness consequences of different forms of induced and constitutive resistance, as well as the effects of a phenological mismatch between larvae and birch, are also well documented [16].

(b) Life-history optimization in Epirrita autumnata

We implemented the life of female *E. autumnata* as a model that was used to solve the optimal timing and duration of its life-history events. Different stages of life were subject to predation and other known fitness-reducing factors in a manner that was dependent on the duration of these life stages. In order to account for variable combinations of season length and predation, the model followed the life stages of *E. autumnata* throughout two successive generations (figure 1). The model runs began with the first generation at the egg stage in the spring of the first year and ended with the oviposition of eggs by the second generation in the autumn of the second year. The final number of oviposited eggs (both male and female) left to overwinter at the end of the second generation was used as the final fitness measure f, such that

$$f = N_1 N_2,$$

where N_1 is the number of female eggs produced and surviving after the egg stage in the first season:

$$N_1 = 0.5(1 - M_s M_l M_p M_o M_a) R_o,$$

where the different M_s are the integral values of the mortality rates for the successive life stages indicated in figure 1 and calculated for the given duration and timing of the life stages within the given length of the first season. R_o is the integral of oviposition rate calculated for the duration of the adult period. Equations and parameterization for the rates are shown in the electronic supplementary material.

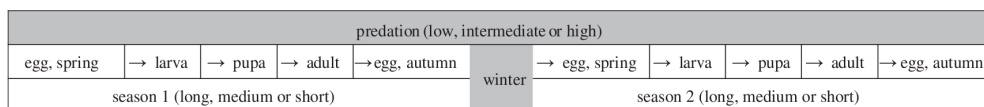| predation (low, intermediate or high)										
egg, spring	→ larva	→ pupa	→ adult	→egg, autumn	winter	→ egg, spring	→ larva	→ pupa	→ adult	→egg, autumn
season 1 (long, medium or short)						season 2 (long, medium or short)				

Figure 1. Life stages for which durations were optimized under different combinations of successive season lengths and predation level. Predation was always equal for both seasons.

The equivalent formula giving the number of both male and female eggs left to overwinter during the second season (N_2) is

$$N_2 = (1 - M_s M_l M_p M_o M_a) R_o,$$

where the M_s are the integral values of mortality rates during the second season and R_o is the integral of the oviposition rate.

The model was used to maximize f by means of resolving the optimal timing and duration of the moth's life history, beginning with the egg in the spring, and proceeding to the larva, pupa, adult and oviposited egg in the autumn. In the model, time was measured in degree days above the threshold of 2°C (dd2).

The maximization of egg number f in the model constituted an MO problem because it was influenced by a set of alternative combinations of life-stage durations that could be optimized with respect to the prevailing season length and predation levels. The mortality rates were varied in different scenarios, in order to account for the variable rates of parasitism and predation that *E. autumnata* experiences during the different stages of its periodic population cycle (the electronic supplementary material). In order to simplify the calculations, we assumed a constant low-, intermediate- or high-mortality rate for all the life stages in a single simulation. This corresponds to mortality rates between the population peaks, shortly before a population crash, and during and shortly after a population crash, respectively.

Two seasons were considered adequate for each optimization scenario. In *E. autumnata*, the timing of life-history events during two successive seasons shows close coupling with each other owing to the potentially strong effect of autumnal oviposition date on larval hatching time in spring [17]. The predation levels are also likely to remain relatively constant for most 2-year slices of the full population cycle of *E. autumnata*. There was no good justification for examining longer time periods because there would have been a very large number of different combinations of successive season lengths attempting to track the random fluctuations of actual weather. For the same reason, we deliberately chose not to seek a single global optimum for the timing of life-history events during an entire population cycle. It would have been meaningless also owing to the fact that most of the successive outbreaks of *E. autumanata* take place in different geographical locations including many other uncontrolled factors besides season length [14].

(c) Validation of results

As is typical for many ecological study systems, *E. autumnata* shows extreme variation in its characteristics. The duration of its pupal period is a good example, because it shows more than twofold differences among years with consequent effects on the

timing and duration of adult and oviposition period [18], and even on the timing of lar-val hatching in spring [17]. As we wanted to investigate the causes and consequences of such variation with our model, we selected validation data from growth conditions showing as close resemblance with the model scenarios as possible.

Both experimental data and field observations from different sources were used. The basic requirement for experimental data was that multiple broods of *E. autumnata* belonging to the local population were reared in outdoor conditions within the area of the Kevo Subarctic Research Station of the University of Turku, Finland. As the data originated from different years and experiments, it combined the potential phenotypic and genotypic sources of variation in the life-history events. Degree days above the threshold of 2°C (dd2) were used as the unit of time. Both the mean duration of a life stage and a measure of its variation were extracted from each data source (reported here along with the results), sometimes using the original observations instead of values directly reported in the source papers. The values were transformed into dd2 using local weather recordings. The standard deviation was used as the measure of variation. Total season lengths in the validation data were chosen to fall within 100 dd2 of those used in the model, which corresponded to a maximum of 8 to 12 per cent mismatch, depending on a particular model scenario and dataset.

Variation in the duration of larval period was estimated from larval rearings inside mesh bags attached to tree branches. In these rearings, the eggs were made to hatch in close synchrony and larvae were then allowed to feed freely on foliage until pupation approached. To determine the duration of larval period, the final instar larvae were inspected daily and pupating larvae were removed from the bags. This has been a standard rearing method for *E. autumnata* over many years, and is known to result in larval periods and other performance measures that show close correspondence with wild or uncaged larvae [17, 19, 20].

The duration of pupal period was estimated with data reporting the eclosion dates of pupae kept individually in vials supplemented with a small amount of moist Sphagnum moss and stored outdoors. As the eclosion time approached, the vials were checked daily for the emergence of adults to determine the duration of pupal period. This has also been a standard method for many years, and is known to result in pupal periods matching with field-buried pupae and in eclosion dates matching with the capture dates of adult moths in light-traps or pheromone traps [17, 21, 22].

The duration of the adult stage and the time in dd2 spent as eggs in autumn were estimated, determining the time when 50 per cent of the total annual catch of adult moths were captured by light-traps. The restriction was made because adult females can oviposit the majority of their eggs in a shorter time than their lifespan is, or what is indicated by a pooled sample of trapped individuals. The light-trap data were suf-

ficient to indicate the potentially large intra-annual variation in the duration of flight period, which is ultimately limited by the onset of winter [17, 18]. It was not crucial to determine the exact duration of the adult period because it is the timing of eclosion and duration of autumn with their consequences for the next season that count more. Oviposition starts soon after eclosion, and the periods during which the female continues to oviposit and its eggs accumulate thermal sum in autumn overlap both in the field and in our model.

For the duration of the egg stage in spring, which indicates the range for the beginning of the larval period, only a single laboratory value was directly available. However, this was considered a minor problem, because *E. autumnata* hatches during a short period in close synchrony with the burst of mountain birch buds. The laboratory value and its variation fit well into the favourable hatching period that was accounted for in the model (electronic supplementary material) and that has been reported in several experiments [17,23].

The most sensible way of validation was to pool the mean life-stage durations and their standard deviations observed in different sources, and to compare them against the pooled predictions of the model. This was reasonable because the observations usually covered only one season length that was also somewhat variable compared with those used in the model. The pooling of data and predictions ensured that both sets included a well-comparable range of alternative conditions. The match between the model and the observations was quantified by calculating the coefficient of determination (R^2) for predicted versus observed values of each life-stage duration, with the duration being expressed as both its mean value and its standard deviation.

However, in order to detect potential fine-scale discrepancies between the data and model predictions, we also split the observed data approximately into the same season lengths as used in the model and conducted a similar validation procedure for the split results as for the pooled results.

RESULTS

Although the optimization runs permitted a wide parameter space, the optimal duration of *E. autumnata* life stages converged to values well within the range of those observed under field conditions (figure 2; $R^2 = 0.93$ for observed versus predicted means and $R^2 = 0.52$ for s.d.). A reasonable fit remained even when the observed data were split into long, medium and short season lengths (figure 3; $R^2 = 0.89$ for observed versus predicted means and $R^2 = 0.13$ for s.d.). Under short and medium season lengths, the observed duration of the larval stage was slightly longer and the pupal period shorter than the optimum suggested by the model (figure 3). The exact durations of the adult

and egg stages were not precisely defined owing to their overlap. The amount of variation among and within individual scenarios was considerable, often differing by tens of percentage points from the mean, as was also the case in the field (figure 3; electronic supplementary material, Table S2).
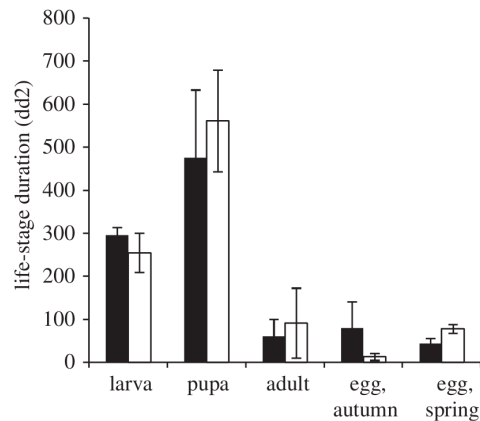

Figure 2. The duration of life stages in *Epirrita autumnata* observed under natural light and temperature regimes, and optimized by a model. The overall means in degree days above 2°C (dd2) are shown. Part of the adult stage duration belongs to the autumn eggs owing to the overlap of these stages. Black bars, observed; white bars, model.

When a coefficient of variation was used to quantify variation (electronic supplementary material, Table S2), the durations of the spring egg and larval stages were least variable within individual scenarios, and the autumn egg stage was the most variable, although the patterns were also dependent on the combinations of season length. The average coefficient of variation in the final fitness values within each scenario was 3 per cent (electronic supplementary material, Table S2), which suggests that the optimization method produced stable and convergent results.

A single sample case where alternative life-stage durations produce an equal fitness is depicted in figure 4, which shows how the duration of the pupal period can be traded with the duration of the adult and autumn egg stages. Another example demonstrates how successive seasons of equal length may produce different optima even for the same predation level: under conditions of short season and high predation risk, there was a 1.5-fold difference in the average optimal duration of the pupal stage, depending on whether duration was optimized for the first (248 dd2) or the second (377 dd2) season (electronic supplementary material, Table S2).

DISCUSSION

In general, the type of phenotypic plasticity predicted by our model in the optimal life-stage durations reflects the ability of individual organisms to alter their life history
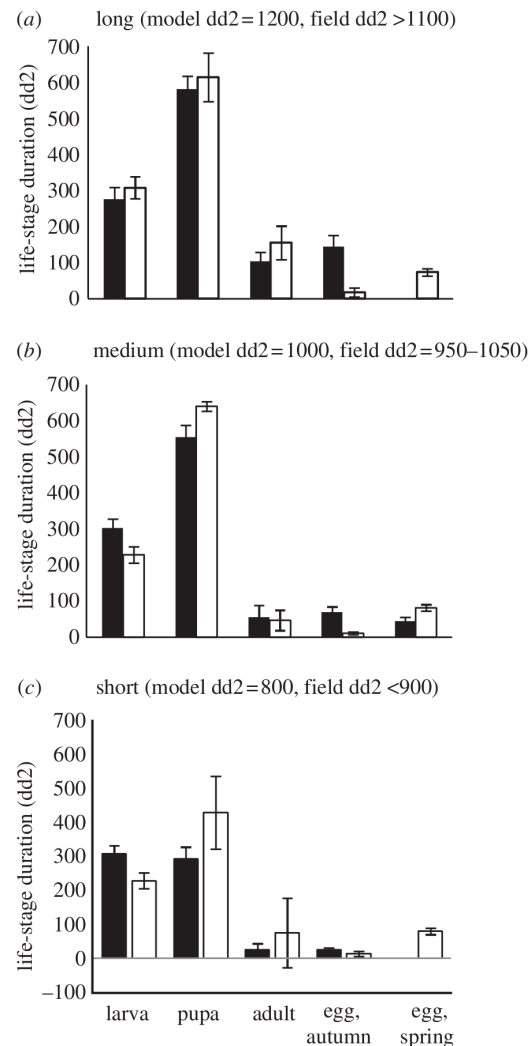
Figure 3. The duration of life stages in *Epirrita autumnata* as observed in field conditions or optimized by a model under different season lengths. Means with standard deviations in degree days above 2°C (dd2) are shown. The observed values are based on brood- or treatment-specific values, depending on the availability of data, and typically relied on recalculation of time in dd2. Sources of observed data are: (a) larva [20], pupa [24]; (b) larva [25], pupa [17]; (c) larva [17, 26], pupa [24]; (a–c) adult and autumn egg [17]. The observed periods spent as adults or autumn eggs were estimated by determining the time when 50% of the total annual adult moths were captured by light-traps ($n = 2$ years each). The duration of spring egg stage in (b) was based on a laboratory value [26]. Part of the adult stage duration belongs to autumn eggs owing to the overlap of these stages. Black bars, observed; white bars, model.

or other vital traits in response to the conditions in which they live. The causes of plasticity may vary, but the unifying explanation is that organisms attempt to optimize their fitness-determining traits with respect to the prevailing environment [5]. This causal relationship may not, however, always be clear, as the plastic responses may show much variation even under identical conditions. In *E. autumnata*, for example, conclusive stage-specific optimization of larval and pupal period has not been observed before. For larval development, Tammaru (p. 86 in [27]) concluded that 'the reaction
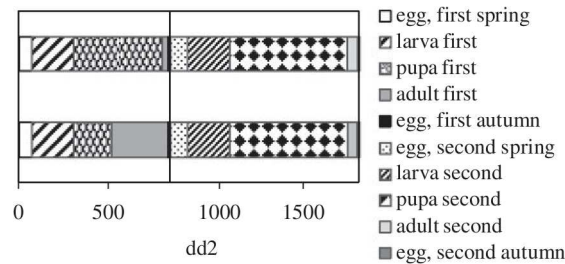
Figure 4. The optimal durations of life stages can be different in alternative solutions to a single steady-state scenario. The predictions were calculated for a short first season and medium second season, and a high predation level. Both solutions produced 0.45 as the final fitness value (electronic supplementary material, Table S2).

norms appeared not to be optimal within the explanatory framework of the model'. For pupal period, Tammaru *et al.* (p. 1674 in [18]) concluded that 'there is a substantial amount of environmental variance in pupal period that is not interpretable as resulting from a deterministic reaction norm, either adaptive or constraint-based. It provides, therefore, a candidate for random environmental variance.'

Our model demonstrated that apparently random variation may not be random after all. On the contrary, variation can be a direct mechanistic consequence of alternative optimal solutions to an MO problem, which sheds light on the potential causes of random variation in life-history traits or, by the same logic, in other fitness-related biological traits [13]. We were very much able to repeat the patterns of variability observed in the duration of life stages in *E. autumnata*, even though the model included only some season lengths combined with a subset of other environmental factors potentially affecting the fitness of *E. autumnata*. There were no unique optimal life-stage durations, but the optima varied greatly according to the change in the combination of season length and mortality risk with each population phase (figure 3; electronic supplementary material, Table S2). In addition, as is typical for solutions in MO, the model predicted alternative optima even in a steady-state situation (figure 4). The most notable discrepancy between the model predictions and the data was that the optimal larval period during the short and medium seasons was shorter than the average observed in the field. However, extending the larval period may be feasible because growing long directly enhances the fecundity of *E. autumnata* [27] and the final season length in dd2 cannot be predicted yet at the larval stage. In an evolutionary time scale consisting of several generations and variable season lengths, the fitness costs of an unnecessarily short larval stage could be more serious than the potential predation risks associated with extending the larval period.

A large amount of variation can persist in the population because the true optima in the field may constantly change according to environmental conditions, and a single strategy would not be optimal to all situations. Variation may appear random and

act as if it serves as an adaptation to random fluctuations of the environment, yet it can have a clear identifiable and quantifiable explanation as our model suggested, and hence also a highly heritable genetic background maintained through associated selective forces in an evolutionary time scale [18]. Although additional explanatory factors could have been incorporated into our model, such as the potential behavioural responses of the moth to its environmental conditions, they would not necessarily have changed the overall predictions. Additional factors might influence alternative optima at a fine scale, but would augment overall variation only if they predicted optima that were outside the values predicted by the current model.

Phenotypic plasticity shows variation also in itself, but the ecological and evolutionary causes and consequences of this variation remain poorly known [5, 28]. Although multiple optima are not a mandatory outcome of MO, our example showed that MO can predict adaptive variation in phenotypes even under stable conditions as very different phenotypes may have equal fitness (figure 4), which has also been demonstrated experimentally in bacteria [29]. It is interesting to note the parallels of this mechanistic prediction with the recent findings of neutral biodiversity theory, which demonstrate that the demographic performance of phenotypically different but trophically similar species coexisting in the same place can be identical on a per capita basis in terms of their rates of birth, death, dispersal and speciation [30]. In essence, neutral theory implicitly assumes that MO may explain inter-specific variation in the traits of coexisting species.

Many aspects of variation and plasticity, along with their genetic and environmental causes, have been examined in the literature. It appears, however, that with the exception of a few sample studies [10–13], the ecological literature has not explicitly considered the potential of multi-objective solutions as a general explanation of variation in the traits of organisms. Although often unexplained and overlooked in experimental studies, variation can serve a clearly interpretable and vital function for organisms. MO can be used as a mathematical method for a strictly mechanistic analysis of the ecological and evolutionary causes and consequences of this variation. Although its efficient usage may involve laborious data collection and require a thorough knowledge of the system under investigation, should not this be a necessary precondition for all mechanistic explanations of functioning in biological systems?

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ELECTRONIC SUPPLEMENTARY MATERIAL

The text here describes the rationalisation and parameterisation of the model in (a) to (d), and shows the average optimisation results of individual model scenarios in Table S2 (e).

(a) Description of the model

Each life history stage was assumed to be subject to a specific mortality rate that reflected the contribution of known mortality factors for *E. autumnata* as a function of dd2s spent in the given stage. It was assumed that a stage-specific, physiologically constrained minimum had to be met during each life stage to ensure normal development, while 700 dd2s was used as a common maximum for all stages. In order to explore the whole parameter space, the minimum and maximum durations of each life stage were well beyond the typical values for *E. autumnata*. Beyond these limits, any values were acceptable on the condition that the total duration of the different stages did not deviate from the total length of the season, which means that the sum of the duration of each life stages always had to match the total season length.

In spring, the eggs of *E. autumnata* are the prey of invertebrate predators [1]. These effects were modelled as a constant density-independent mortality rate per dd2 spent at the egg stage (see (**c**)). The increased mortality risk caused by an asynchronous hatching of eggs in relation to the bud burst of mountain birch was included in the mortality function of the egg stage in spring (**c**). Mortality was considered to increase steeply if hatching occurred before foliage was available on 70 dd2 because the supply of alternative food sources is negligible and the larvae cannot survive without food for long [2]. The time of bud burst in mountain birch shows considerable variation around the mean, but the only means of dispersal for the larvae is ballooning in the wind using a silken thread, which appears to be an inefficient method for locating alternative host trees and results in lowered survival rates where there is increased asynchrony. The total minimum time requirement of 100 dd2s used in the model for egg hatching was lower than that estimated experimentally [3]. Although the accumulation of dd2s required for egg hatching (hatchdd2) may already start in the autumn [3], there is evidence that the eggs of *E. autumnata* undergo a diapauses [4], hence it was assumed that at least 20 dd2s had to be accumulated in spring in order for hatching to take place.

Larval mortality was modelled as a function of hatchdd2 (**c**) because the effects of larval mortality factors depend largely on both the timing of larval hatching and on the timing of the larval stage within the season [3]. The rate of larval mortality in *E. autumnata* can be highly variable, and it is influenced by both invertebrate and vertebrate predators, parasitoids, food quality, and the degree of phenological synchronization

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with the mountain birch [5]. Larval mortality was modelled in a density-dependent manner and accounted for the fact that the chances of survival decline both around population peaks and also when the season progresses and concurrent increases in the rates of parasitism and predation [3] combine with a decrease in food quality [6]. The minimum time requirement for the larval stage was set at 200 dd2s, which was well below the reported 200 dd5s [3]. The density-dependent larval mortality functions were considered adequate also to account for the fitness decrease due to the induced resistance of the host plant to *E. autumnata* larvae [5,6].

In *E. autumnata*, the larval stage also contributes to the maximization of the fitness measure by influencing the number of eggs that an adult can oviposit because the final egg number is directly determined by the weight of female larvae at the time of pupation [7]. The growth rate and timing of different larval instars was estimated on the basis of instar-specific observations [3]. In addition, the function for the larval growth rate was adjusted so that the final larval weight directly corresponded to the actual pupal weight, which allowed us to account for the weight loss of larvae during pupation. Apart from temperature, the larval growth rate mainly depends on the quality of food, including the effect of phenological synchronization between the larvae and their host plant [5]. Hence the larval growth rate was modified by a factor r that controlled the effect of phenological synchrony between the birch bud burst and the egg hatching of *E. autumnata* as a function of the larval hatching time:

$$r = 1 - 0.0000001 hatchdd2^3 \qquad (1)$$

Thus, in the function for determining the growth rate (w), the delayed hatching of eggs results in delayed larval development in relation to birch leaves [3] and a consequent decrease in the growth rate and final weight of larvae and pupae modelled as

$$w = 0.05 r \, e^{-0.008(1-dd2)} \qquad (2)$$

The maximum egg number was calculated as a function of pupal weight w_p [8] which equals the integrated value of w.

$$N_0 = -37.27 + 2.33 w_p \qquad (3)$$

It was assumed that females weighing less than 30 mg as pupae were not capable of producing any eggs ($N_0 = 0$, if $w_p < 30$ mg), as observed in the laboratory.

Pupal mortality is also affected by the rates of predation and parasitism [9,10] and was modelled as constant density-dependent rates per dd2 (**c**). The minimum requirement for completing the pupal stage was set at 200 dd2s, which is below the average

time required for the first signs of fully developed adult structure to develop in the pupae of *E. autumnata* [11].

During the adult stage, survival per dd2 was assumed to increase towards the end of the season due to decreasing predator activity (**c**). Adults started oviposition at the minimum age of 10 dd2s and were assumed to lay their eggs at a rate $r_o = 1$ egg/ dd2 (also including the daytime accumulation of dd2s) [7]. In addition to the oviposition rate, the outcome of oviposition was affected by the simultaneous effects of adult and egg mortality [1]. The age differences of eggs produced in the course of the oviposition period were not considered in the optimisation. It was assumed that all the eggs started to accumulate dd2s for hatching only after the oviposition of the last eggs, which means that a fraction of the adult period must also be added to those eggs already laid.

The calculation of adult mortality was based on results that use calendar days instead of dd2s [7, 12]. Therefore, to estimate the effect of dd2s on adult mortality, we used the long-term average of daily dd2s in the autumn to construct a function that translated calendar days into dd2s (**c**). Adult mortality was assumed to be lowest during population peaks, due to inversely density-dependent predation by generalist predators. Harvestmen (Opiliones) are the main source of mortality, with predator saturation increasing with prey density [12].

The model that calculated the final fitness value included the female eggs N_1 produced and surviving after the egg stage in the first season

$$N_1 = 0.5(1 - M_s M_l M_p M_o M_a)R_o \qquad (4)$$

where capitalized M_s are the integral values of the mortality rates given in (**c**) and calculated for the given duration and timing of the life stages within the given length of the first season. R_o is the integral of oviposition rate r_o calculated for the duration of the adult period. The maximum value of R_o was limited by the maximum egg number N_o determined by equation (3).

The equivalent formula giving the number of both male and female eggs left to overwinter during the second season (N_2) is

$$N_2 = (1 - M_s M_l M_p M_o M_a)R_o \qquad (5)$$

where the capitalized M_s are the integral values of mortality rates during the second season and R_o is the integral of the oviposition rate with its maximum limited by N_o.

Accordingly, the final fitness measure f for optimisation becomes

$$f = N_1 N_2 \qquad (6)$$

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(b) Optimisation scenarios

The duration and timing of the life stages was optimised in 27 different scenarios produced by the factorial arrangement of season lengths and mortality rates. The total season lengths for the two successive seasons were varied within previously observed limits obtained from daily temperature measurements recorded at the Kevo Subarctic Research Station and reaching back to 1962. Here 800 dd2s was classified as a short season, 1.000 dd2s a medium and 1.200 dd2s a long season. The three classes of mortality rate constituted another part of the environmental variation in the optimisation scenarios.

In spite of the simplifications, the search space consisted of more than 2×1.015 alternative combinations of season length, mortality class and life stage duration. We used Evolver 4.0 genetic algorithm solver (Palisade Corporation, Newfield, NY, USA) to search for the optimal solutions using ordinary PCs. Eleven optimisation runs were conducted for each scenario using the software's default solving methods. A single solution was considered final when there was less than 5% improvement on the solution for the next 400 successive runs.

The model was validated by comparing the predicted timings and durations of the life stages with the values observed in *E. autumnata* that experienced a natural light and temperature regime during different season lengths and population phases.

(c) Mortality functions used in the model

Table S1.

Life stage	mortality rate / dd2		
	low	*intermediate*	*high*
spring egg, m_s	0.0002, if $hatchdd2 \geq 70$	0.0002, if $hatchdd2 \geq 70$	0.0002, if $hatchdd2 \geq 70$
	$0.0002 + 1 - \mathrm{e}^{-0.03(70-hatchdd2)}$, if $hatchdd2 < 70$	$0.0002 + 1 - \mathrm{e}^{-0.03(70-hatchdd2)}$, if $hatchdd2 < 70$	$0.0002 + 1 - \mathrm{e}^{-0.03(70-hatchdd2)}$, if $hatchdd2 < 70$
larva, m_l	$0.0015\mathrm{e}^{0.004(hatchdd2-130)}$	$0.002\mathrm{e}^{0.004(hatchdd2-130)}$	$0.0025\mathrm{e}^{0.004(hatchdd2-130)}$
pupa, m_p	$1 - 0.9993^{dd2}$	$1 - 0.99895^{dd2}$	$1 - 0.0.99860^{dd2}$
adult, m_o	$0.6\mathrm{e}^{-\left[\frac{dd2-500}{400}\right]^5}$	$0.4\mathrm{e}^{-\left[\frac{dd2-500}{400}\right]^5}$	$0.2\mathrm{e}^{-\left[\frac{dd2-500}{400}\right]^5}$
autumn egg, m_a	$0.006 - 0.0000044\,dd2$	$0.015 - 0.000012\,dd2$	$0.025 - 0.00002\,dd2$

(d) References

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(e) Optimisation results

Table S2. The final fitness values and optimal life stage durations during two successive years in individual model scenarios. The length of years and life stages are given in dd2s. The mean values and their coefficients of variation are based on 11 optimisation runs.

Predation	1st year	2nd year	Variable	Mean	CV
high	800	800	fitness	0.030	4.211
			egg, 1st spring	71.182	1.969
			larva, 1st summer	221.000	0.000
			pupa, 1st summer	248.273	43.261
			adult 1st autumn	247.455	43.096
			egg, 1st autumn	12.091	43.522
			egg, 2nd spring	88.000	6.035
			larva, 2nd summer	224.455	0.576
			pupa, 2nd summer	376.727	30.130
			adult, 2nd autumn	100.727	117.173
			egg, 2nd autumn	10.091	2.988
high	800	1000	fitness	0.434	6.089
			egg, 1st spring	70.818	2.077
			larva, 1st summer	221.000	0.000
			pupa, 1st summer	294.818	44.644
			adult 1st autumn	199.727	66.310
			egg, 1st autumn	13.636	36.116
			egg, 2nd spring	86.545	5.877
			larva, 2nd summer	224.273	0.567
			pupa, 2nd summer	626.545	1.030
			adult, 2nd autumn	52.273	1.930
			egg, 2nd autumn	10.364	11.6370
high	800	1200	fitness	2.097	4.356
			egg, 1st spring	70.727	1.561
			larva, 1st summer	221.000	0.000
			pupa, 1st summer	223.364	34.692
			adult 1st autumn	253.636	29.125
			egg, 1st autumn	31.273	27.362
			egg, 2nd spring	68.727	12.450
			larva, 2nd summer	327.727	0.627
			pupa, 2nd summer	603.364	1.776
			adult, 2nd autumn	187.909	1.457
			egg, 2nd autumn	12.273	23.073
high	1000	800	fitness	0.422	9.502
			egg, 1st spring	71.909	2.672
			larva, 1st summer	221.182	0.183
			pupa, 1st summer	643.000	0.582
			adult 1st autumn	51.273	3.388

Table S2. (continued)

Predation	1st year	2nd year	Variable	Mean	CV
			egg, 1st autumn	12.636	39.453
			egg, 2nd spring	87.545	5.833
			larva, 2nd summer	224.273	0.531
			pupa, 2nd summer	394.364	24.572
			adult, 2nd autumn	83.818	122.931
			egg, 2nd autumn	10.000	0.000
high	1000	1000	fitness	3.893	2.880
			egg, 1st spring	71.818	3.674
			larva, 1st summer	221.182	0.273
			pupa, 1st summer	622.727	0.575
			adult 1st autumn	42.818	2.041
			egg, 1st autumn	10.455	14.420
			egg, 2nd spring	89.545	1.684
			larva, 2nd summer	225.000	0.199
			pupa, 2nd summer	622.727	0.352
			adult, 2nd autumn	52.727	2.557
			egg, 2nd autumn	10.000	0.000
high	100	1200	fitness	30.436	10.256
			egg, 1st spring	75.273	8.256
			larva, 1st summer	221.727	0.608
			pupa, 1st summer	635.364	1.681
			adult 1st autumn	51.273	8.639
			egg, 1st autumn	16.364	47.515
			egg, 2nd spring	83.636	9.296
			larva, 2nd summer	332.273	0.726
			pupa, 2nd summer	586.636	1.693
			adult, 2nd autumn	186.727	2.311
			egg, 2nd autumn	10.727	14.496
high	1200	800	fitness	2.454	2.873
			egg, 1st spring	70.091	0.430
			larva, 1st summer	318.455	1.664
			pupa, 1st summer	609.909	0.760
			adult 1st autumn	172.182	5.122
			egg, 1st autumn	29.364	32.102
			egg, 2nd spring	70.636	13.345
			larva, 2nd summer	221.364	0.763
			pupa, 2nd summer	343.727	40.102
			adult, 2nd autumn	154.273	91.520
			egg, 2nd autumn	10.000	0.000
high	1200	1000	fitness	36.775	3.589
			egg, 1st spring	70.091	0.430
			larva, 1st summer	324.000	1.751

Table S2. (continued)

Predation	1st year	2nd year	Variable	Mean	CV
			pupa, 1st summer	605.636	1.063
			adult 1st autumn	180.818	6.566
			egg, 1st autumn	19.455	56.885
			egg, 2nd spring	80.545	13.740
			larva, 2nd summer	223.091	0.884
			pupa, 2nd summer	633.727	2.055
			adult, 2nd autumn	52.636	2.587
			egg, 2nd autumn	10.000	0.000
high	1200	1200	fitness	197.998	2.615
			egg, 1st spring	70.182	0.576
			larva, 1st summer	312.636	2.767
			pupa, 1st summer	613.455	1.016
			adult 1st autumn	164.545	7.244
			egg, 1st autumn	39.182	36.876
			egg, 2nd spring	60.818	23.757
			larva, 2nd summer	325.909	0.375
			pupa, 2nd summer	612.091	2.692
			adult, 2nd autumn	187.909	4.581
			egg, 2nd autumn	13.273	36.615
intermediate	800	800	fitness	0.001	0.465
			egg, 1st spring	71.818	2.141
			larva, 1st summer	221.000	0.000
			pupa, 1st summer	476.455	0.368
			adult 1st autumn	20.636	2.445
			egg, 1st autumn	10.091	2.988
			egg, 2nd spring	90.091	0.599
			larva, 2nd summer	225.273	0.207
			pupa, 2nd summer	454.182	0.257
			adult, 2nd autumn	20.455	2.553
			egg, 2nd autumn	10.000	0.000
intermediate	800	1000	fitness	0.048	1.258
			egg, 1st spring	71.636	2.187
			larva, 1st summer	221.000	0.000
			pupa, 1st summer	476.455	0.330
			adult 1st autumn	20.636	2.445
			egg, 1st autumn	10.273	8.805
			egg, 2nd spring	89.818	1.093
			larva, 2nd summer	225.091	0.240
			pupa, 2nd summer	637.364	0.256
			adult, 2nd autumn	37.727	1.238
			egg, 2nd autumn	10.000	0.000
intermediate	800	1200	fitness	0.489	6.194

Table S2. (continued)

Predation	1st year	2nd year	Variable	Mean	CV
			egg, 1st spring	71.273	1.892
			larva, 1st summer	221.000	0.000
			pupa, 1st summer	472.818	1.177
			adult 1st autumn	20.727	3.120
			egg, 1st autumn	14.182	37.154
			egg, 2nd spring	85.818	6.140
			larva, 2nd summer	324.364	0.372
			pupa, 2nd summer	612.364	1.303
			adult, 2nd autumn	167.455	1.718
			egg, 2nd autumn	10.000	0.000
intermediate	1000	800	fitness	0.048	0.635
			egg, 1st spring	74.273	5.963
			larva, 1st summer	221.636	0.365
			pupa, 1st summer	656.364	0.810
			adult 1st autumn	37.727	2.084
			egg, 1st autumn	10.000	0.000
			egg, 2nd spring	90.182	0.449
			larva, 2nd summer	225.182	0.268
			pupa, 2nd summer	453.909	0.250
			adult, 2nd autumn	20.727	2.254
			egg, 2nd autumn	10.000	0.000
intermediate	1000	1000	fitness	6.344	1.260
			egg, 1st spring	74.000	5.506
			larva, 1st summer	221.364	0.365
			pupa, 1st summer	656.636	0.695
			adult 1st autumn	37.818	1.985
			egg, 1st autumn	10.182	5.923
			egg, 2nd spring	89.818	0.671
			larva, 2nd summer	225.364	0.359
			pupa, 2nd summer	636.455	0.301
			adult, 2nd autumn	38.364	2.109
			egg, 2nd autumn	10.000	0.000
intermediate	1000	1200	fitness	43.451	1.148
			egg, 1st spring	75.909	5.816
			larva, 1st summer	221.909	0.425
			pupa, 1st summer	654.364	0.843
			adult 1st autumn	37.727	1.238
			egg, 1st autumn	10.091	2.988
			egg, 2nd spring	89.909	0.335
			larva, 2nd summer	325.455	0.160
			pupa, 2nd summer	607.000	0.410
			adult, 2nd autumn	167.636	1.629

Table S2. (continued)

Predation	1st year	2nd year	Variable	Mean	CV
			egg, 2nd autumn	10.000	0.000
intermediate	1200	800	fitness	0.538	1.120
			egg, 1st spring	70.000	0.000
			larva, 1st summer	320.000	0.559
			pupa, 1st summer	633.455	0.216
			adult 1st autumn	165.000	1.355
			egg, 1st autumn	11.545	24.303
			egg, 2nd spring	88.727	3.422
			larva, 2nd summer	224.727	0.350
			pupa, 2nd summer	455.909	0.923
			adult, 2nd autumn	20.636	2.445
			egg, 2nd autumn	10.000	0.000
intermediate	1200	1000	fitness	45.290	2.674
			egg, 1st spring	70.273	0.920
			larva, 1st summer	318.364	1.091
			pupa, 1st summer	633.364	0.735
			adult 1st autumn	164.000	4.225
			egg, 1st autumn	14.000	42.378
			egg, 2nd spring	86.000	6.899
			larva, 2nd summer	224.545	0.576
			pupa, 2nd summer	642.182	1.103
			adult, 2nd autumn	37.273	1.735
			egg, 2nd autumn	10.000	0.000
intermediate	1200	1200	fitness	456.051	5.445
			egg, 1st spring	70.091	0.430
			larva, 1st summer	304.000	2.573
			pupa, 1st summer	644.455	1.107
			adult 1st autumn	144.091	7.970
			egg, 1st autumn	37.364	33.068
			egg, 2nd spring	62.636	19.726
			larva, 2nd summer	319.364	0.770
			pupa, 2nd summer	640.091	2.171
			adult, 2nd autumn	166.909	1.662
			egg, 2nd autumn	11.000	20.328
low	800	800	fitness	0.000	0.168
			egg, 1st spring	72.636	1.273
			larva, 1st summer	221.000	0.000
			pupa, 1st summer	479.364	0.193
			adult 1st autumn	17.000	0.000
			egg, 1st autumn	10.000	0.000
			egg, 2nd spring	90.091	0.335
			larva, 2nd summer	225.182	0.180

Table S2. (continued)

Predation	1st year	2nd year	Variable	Mean	CV
			pupa, 2nd summer	457.636	0.147
			adult, 2nd autumn	17.091	1.764
			egg, 2nd autumn	10.000	0.000
low	800	1000	fitness	0.008	0.121
			egg, 1st spring	72.000	2.060
			larva, 1st summer	221.000	0.000
			pupa, 1st summer	480.000	0.309
			adult 1st autumn	17.000	0.000
			egg, 1st autumn	10.000	0.000
			egg, 2nd spring	90.000	0.000
			larva, 2nd summer	225.545	0.305
			pupa, 2nd summer	643.455	0.127
			adult, 2nd autumn	31.000	1.443
			egg, 2nd autumn	10.000	0.000
low	800	1200	fitness	0.132	4.626
			egg, 1st spring	72.273	5.938
			larva, 1st summer	221.273	0.409
			pupa, 1st summer	477.182	1.147
			adult 1st autumn	17.182	3.510
			egg, 1st autumn	12.091	24.100
			egg, 2nd spring	87.909	3.315
			larva, 2nd summer	323.364	3.464
			pupa, 2nd summer	623.636	2.338
			adult, 2nd autumn	155.091	1.717
			egg, 2nd autumn	10.000	0.000
low	1000	800	fitness	0.008	0.315
			egg, 1st spring	73.000	4.155
			larva, 1st summer	221.455	0.422
			pupa, 1st summer	664.636	0.599
			adult 1st autumn	30.909	0.975
			egg, 1st autumn	10.000	0.000
			egg, 2nd spring	90.091	0.335
			larva, 2nd summer	225.091	0.134
			pupa, 2nd summer	457.818	0.132
			adult, 2nd autumn	17.000	0.000
			egg, 2nd autumn	10.000	0.000
low	1000	1000	fitness	3.497	0.817
			egg, 1st spring	76.091	10.154
			larva, 1st summer	222.000	0.726
			pupa, 1st summer	660.909	1.410
			adult 1st autumn	31.000	1.443
			egg, 1st autumn	10.000	0.000

Table S2. (continued)

Predation	1st year	2nd year	Variable	Mean	CV
			egg, 2nd spring	90.000	0.000
			larva, 2nd summer	225.182	0.180
			pupa, 2nd summer	644.000	0.098
			adult, 2nd autumn	30.818	1.313
			egg, 2nd autumn	10.000	0.000
low	1000	1200	fitness	61.752	0.711
			egg, 1st spring	77.364	8.753
			larva, 1st summer	222.455	0.788
			pupa, 1st summer	659.182	1.287
			adult 1st autumn	31.000	0.000
			egg, 1st autumn	10.000	0.000
			egg, 2nd spring	90.000	0.000
			larva, 2nd summer	320.909	0.645
			pupa, 2nd summer	622.091	0.468
			adult, 2nd autumn	157.000	1.066
			egg, 2nd autumn	10.000	0.000
low	1200	800	fitness	0.139	1.635
			egg, 1st spring	70.000	0.000
			larva, 1st summer	318.545	1.783
			pupa, 1st summer	644.727	0.949
			adult 1st autumn	155.636	2.136
			egg, 1st autumn	11.091	27.185
			egg, 2nd spring	88.909	3.391
			larva, 2nd summer	225.182	0.519
			pupa, 2nd summer	458.909	0.852
			adult, 2nd autumn	17.000	0.000
			egg, 2nd autumn	10.000	0.000
low	1200	1000	fitness	63.658	0.167
			egg, 1st spring	70.091	0.430
			larva, 1st summer	316.000	0.000
			pupa, 1st summer	648.364	0.232
			adult 1st autumn	155.545	0.926
			egg, 1st autumn	10.000	0.000
			egg, 2nd spring	90.182	0.449
			larva, 2nd summer	225.636	0.359
			pupa, 2nd summer	643.182	0.153
			adult, 2nd autumn	31.000	2.040
			egg, 2nd autumn	10.000	0.000
low	1200	1200	fitness	1035.280	5.414
			egg, 1st spring	70.182	0.576
			larva, 1st summer	306.364	2.400
			pupa, 1st summer	654.182	0.947

Table S2. (continued)

Predation	1st year	2nd year	Variable	Mean	CV
			adult 1st autumn	142.636	6.122
			egg, 1st autumn	26.636	39.385
			egg, 2nd spring	73.364	14.300
			larva, 2nd summer	318.273	1.633
			pupa, 2nd summer	643.455	2.456
			adult, 2nd autumn	154.909	0.977
			egg, 2nd autumn	10.000	0.000