Multi-objective optimization shapes ecological variation

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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

1. 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 alternatives are presented in terms of phenotypic 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 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 pay-offs 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.

2. MATERIAL 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; Hämët-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

\[
f = N_1N_2;
\]

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

\[
N_1 = 0.5(1 - M_1M_2M_3M_4)R_o,
\]

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.

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

\[
N_2 = (1 - M_5M_6M_7M_8)R_o,
\]

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.

<table>
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<tr>
<th>phenotypic life-history strategy.</th>
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<tr>
<td><strong>Oviposition</strong></td>
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<td><strong>Pupa</strong></td>
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<td><strong>Winter</strong></td>
<td><strong>Egg, Autumn</strong></td>
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<tr>
<td><strong>Season 1 (Long, Medium or Short)</strong></td>
<td><strong>Season 2 (Long, Medium or Short)</strong></td>
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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 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. autumnata* 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 larval 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 sufficient 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
and convergent results. The optimization method produced stable (electronic supplementary material, table S2), which suggests that the optimization method produced stable and convergent results.

The average coefficient of variation in the patterns were also dependent on the combinations of season lengths. The average coefficient of variation (electronic supplementary material, table S2), 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 life-stage duration (dd2)

<table>
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<tr>
<th>Season</th>
<th>Model dd2</th>
<th>Field dd2</th>
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<tbody>
<tr>
<td>Long</td>
<td>1200</td>
<td>&gt;1100</td>
</tr>
<tr>
<td>Medium</td>
<td>1000</td>
<td>950–1050</td>
</tr>
<tr>
<td>Short</td>
<td>800</td>
<td>&lt;900</td>
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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.

3. 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.

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 life-stage duration (dd2)
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?

![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).](image-url)
We thank all the numerous field assistants of *E. autumnata* studies who have contributed to the collection of data required in this paper. Kevo Subarctic Research Station provided the necessary facilities and R. Heikkinen provided access to the weather data. Toomas Tammaru gave valuable comments on an earlier version of this manuscript. Comments by anonymous referees helped to improve the paper considerably. The authors T.K. and A.S. were funded by the Academy of Finland.

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