On the status of the scarce fritillary *Euphydryas maturna* (Lepidoptera: Nymphalidae) in Finland

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The scarce fritillary *Euphydryas maturna* (L.) is a highly endangered species of butterfly in several European countries. However, in Finland it occurs commonly in the southeastern part of the country and its distribution has remained stable over the past 40 years. The ecology of *E. maturna* has recently been studied in Finland. In this paper, I review these studies and show that the distribution of the species is tightly linked to its ecology, which differs substantially from the ecology of the same species in central Europe. In Finland, the main larval host plant is *Melampyrum pratense* (Orobanchaceae), which is common throughout Finland. *Euphydryas maturna* is restricted to south facing forest edges where the sharp ecotone provides a warm habitat. Larvae need warm microhabitats to be able to grow fast in the spring. Natural forest edges are formed by rocky outcrops, which are common in SE Finland. The distribution of *E. maturna* coincides with the area where rocky outcrops are common. I suggest that the presence of the granite bedrock close to the surface of the ground largely explains the present distribution of *E. maturna* in Finland. I also note that the species benefits from clearcuts made in the forests and conclude that *E. maturna* is not threatened in Finland at the moment.

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1. Introduction

The scarce fritillary *Euphydryas maturna* (L.) ranges from Europe through Central Asia to Mongolia (Higgins 1950). In Europe, *E. maturna* has declined in many countries over the past few decades (van Swaay & Warren 1999). It has become extinct in Belgium and Luxemburg and populations have decreased by over 75% in Germany, France, Sweden, the Czech Republic and Austria (van Swaay & Warren 1999). The species is protected in all EU countries under the 1992 European Community Council Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (EU directive 92/43/EEC). However, *E. maturna* is still a relatively common species in SE Finland (Fig. 1), though the reasons why it is restricted to this area have not been entirely clear. It has been suggested that populations of the species have been declining in recent years (Marttila *et al.* 1999), though a reanalysis of the data shows no evidence for this (Martikainen & Kouki 1999). Also a recent atlas of the Lepidoptera in Finland shows that the distribution of *E. maturna* has remained stable over several decades (Huldén *et al.* 2000; Fig. 1).

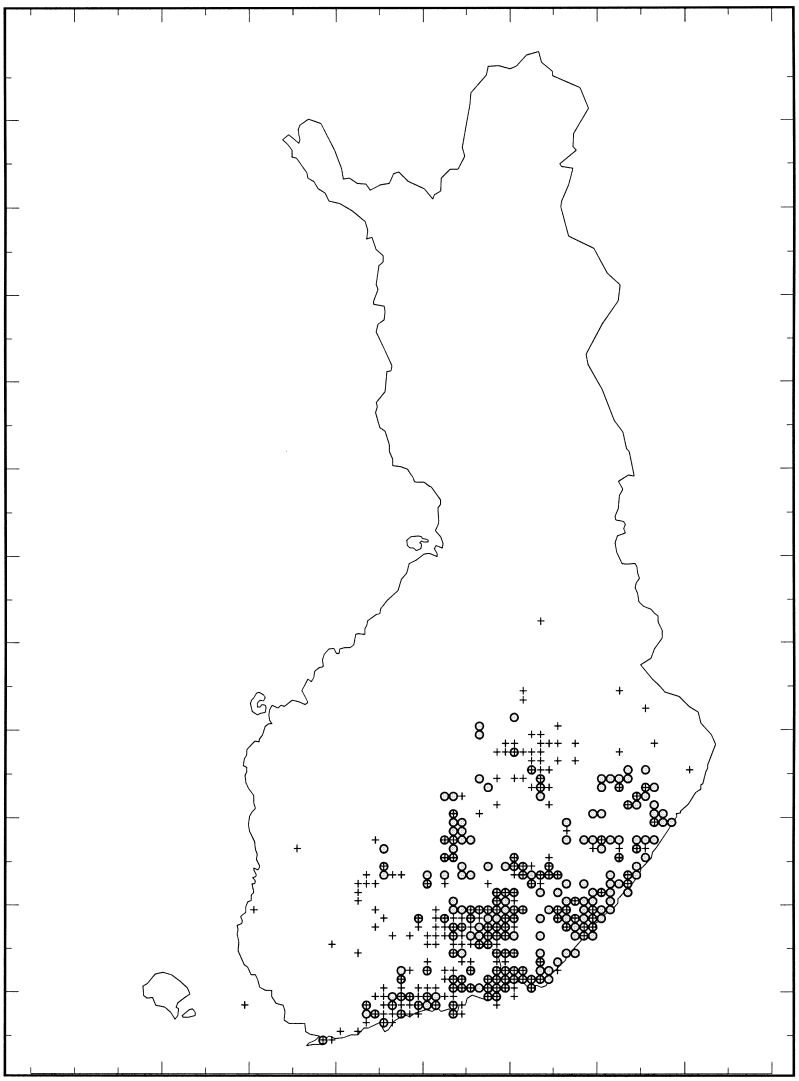

Fig. 1. The distribution of *Euphydryas maturna* in Finland. The crosses represent records of the species prior to 1988 and the circles represent records from 1988–1997. Modified from Huldén *et al.* (2000).

Until recently the ecology of *E. maturna* was not known in Finland and Finnish literature on endangered species (e.g. Somerma 1997) has relied on accounts of the species' ecology from other countries (e.g. Ebert 1991, Eliasson 1991). The ecology of butterfly species, particularly the host plant species utilized, can change much over a scale similar to the size of European countries (e.g. Singer 1983). In the past few years *E. maturna* has been studied in Finland (Komonen 1997, Selonen 1997, Wahlberg 1998, 1999), showing that the species' ecology differs in some crucial aspects from the populations in other countries.

In this paper, I review what is known about the ecology of *E. maturna* in Finland and discuss the effects of the ecology of the species on its habitat requirements in Finland and through that arrive at an explanation for the distribution of the species in Finland. I follow Judd *et al.* (1999) for the familial classification of host plants.

2. Ecology

Euphydryas maturna is known as a species that is found along forest edges, where it occurs in small colonies (Weidemann 1988, Ebert 1991, Eliasson 1991, Marttila *et al.* 1991). The flight period of

the adults lasts for about a month from mid-June to mid-July. Males use the perching tactic to search for females to mate with, that is, they set up temporary territories on prominent pieces of vegetation on which they sit and wait for females to fly past (Wahlberg 1998). Females generally mate once (Wahlberg 1998).

The biology of the larvae is quite remarkable. In Sweden, Germany and the Czech Republic, the eggs are laid on large bushes or small trees of the species *Fraxinus excelsior* L. (Oleaceae) (Weidemann 1988, Ebert 1991, Eliasson 1991, Vrabec & Jindra 1998, Pretscher 2000), *Fraxinus angustifolia* L. (Tolman & Lewington 1997) and occasionally *Viburnum opulus* L. (Adoxaceae) (Eliasson 1991). The larvae then fall to the ground in autumn, where they diapause. In spring the postdiapause larvae feed mainly on herbs such as *Melampyrum pratense* L. (Orobanchaceae) seedlings in Sweden (C. Wiklund pers. comm.), *Plantago* spp. and *Veronica* spp. (both in Plantaginaceae) in Germany (Pretscher 2000), or on small bushes such as *Lonicera xylosteum* L. (Caprifoliaceae) and *Ligustrum vulgare* L. (Oleaceae) in Germany (Pretscher 2000). The range of growth forms of the different host plants is exceptional. However, all plant species mentioned contain secondary compounds known as iridoid glycosides (Jensen *et al*. 1975), on which species of *Euphydryas* apparently specialize (Bowers 1983, Zimmermann *et al*. 2000, Wahlberg 2001).

In contrast to other European countries, the main larval host plant of *E. maturna* in Finland is the herb *Melampyrum pratense*, upon which females lay their eggs in batches of up to 320 (Wahlberg 1998, 1999). Larvae hatch around the beginning of August in Finland and feed in a tight group until diapause (Wahlberg 1998). The larvae spin a conspicuous silken web around the host plant, which can be surveyed easily much like in the related species the Glanville fritillary *Melitaea cinxia* (L.) (Thomas & Simcox 1982, Hanski *et al*. 1995). *Euphydryas maturna* larvae diapause in the 3rd and 4th instar in the leaf litter at the base of their host plant. In spring the larvae can be found basking in groups immediately after snowmelt. In Finland the postdiapause larvae feed mainly on the seedlings of their annual host plant (*M. pratense*), and one larva is able to eat several tens of seedlings in one day (Wahlberg 1998). Thus the larvae must disperse soon after terminating diapause to feed singly.

Other host plant records in Finland are rare. There are single records of larval groups on *Veronica longifolia* L. (Plantaginaceae) and *Viburnum opulus* (Wahlberg 1998, 1999). Postdiapause larvae can occassionally be found on small bushes of *L. xylosteum* (L. Kaila and G. Nordenswan pers. comm.). There is one verified observation of two postdiapause larvae feeding on recently expanded leaves of *Populus tremula* L. (Salicaceae) and one larvae feeding on *Betula pubescens* L. (Betulaceae) in eastern Finland (T. Salin pers. comm.). All three larvae were found at about 1.5 m height and were feeding actively while being observed. The importance of these two trees as host plants is at best marginal as I have never seen them being fed on in my own observations of hundreds of larvae (Wahlberg 1998, 1999, pers. obs.).

Populus tremula is often listed as a host plant of *E. maturna* (Weidemann 1988, Ebert 1991, Tolman & Lewington 1997, Pretscher 2000), but I have been unable to find any verified observations of pre- or postdiapause larvae feeding on this plant in the literature. The main host plant in Finland, *M. pratense*, is a generalist root hemiparasite that parasitizes the roots of a large number of herbaceous and woody plants, especially trees (coniferous and deciduous) and ericaceous shrubs in the boreal region (Gauslaa 1990, Salonen *et al*. 2000). As hemiparasites are able to take up secondary chemicals from their host plants (e.g. Stermitz *et al*. 1989), one can speculate that *E. maturna* larvae are exposed to the secondary chemicals of plants that do not contain iridoid glycosides (e.g. *P. tremula*) and thus may be able to utilize such plants for growth and development. This hypothesis obviously needs to be tested in a rigorous fashion.

Euphydryas maturna has a facultative two year life cycle in Finland and probably in Sweden (Eliasson 1991, Wahlberg 1998), in contrast to more southern populations which normally develop in one year (Z. Varga pers. comm.). The crucial determinant of the length of the life cycle is the growth of the larvae in spring. Larvae that grow fast enough to reach the sixth (= ultimate) instar by the middle of May are able to pupate and thus complete their life cycle in one year (Wahlberg 1998). If the larvae do not reach the

ultimate instar in time, they return to diapause for the rest of the year and become active again the next spring. It is thus possible to find larvae of two age classes in spring.

In Finland, the larvae are attacked by three species of parasitoids: *Cotesia acuminata* (Reinhard) and *C. melitaearum* (Wilkinson) (Hymenoptera: Braconidae), as well as *Erycia fatua* (Meigen) (Diptera: Tachinidae) (Komonen 1997). The importance of the two braconids to the population dynamics of *E. maturna* are unknown, though *C. melitaearum* is known to cause extinctions of local populations of *M. cinxia* (Lei & Hanski 1997). I have reared many *E. fatua* flies from post-diapause larvae and seen adult flies ovipositing on nests of prediapause larvae (Wahlberg 1998). It may be that the dipteran parasitoid has a major impact on the population dynamics of *E. maturna*, though this requires further study.

The population structure and dynamics of *E. maturna* have not been studied explicitly in Finland or any other area. In a mark-recapture study performed in Finland in 1996, it was apparent that the species occured very patchily in the study area of about 4 km^2 (Selonen 1997). The population sizes in these patches were very small, on the order of tens to hundreds of individuals. Very few movements between patches were recorded and these were usually only to the neighbouring patch.

3. Habitat requirements

Euphydryas maturna is a species associated with forest edges and gaps in forests (Marttila *et al.* 1991, Somerma 1997). The precise habitat requirements of the species in Finland have been unknown until recently (Wahlberg 1999). During the course of my studies I have found that there are two main factors that affect the habitat choice of *E. maturna* in Finland. These two factors are the presence of an abundant supply of the main host plant *Melampyrum pratense* and a microclimate that enhances rapid growth of larvae in the spring. The presence of an abundant supply of *M. pratense* is crucial for spring larvae as one larva is able to consume one seedling in a matter of minutes (Wahlberg 1998). One larval group can contain over 100 larvae in autumn and these larvae must then find enough to eat in spring. A very warm microclimate facilitates rapid growth in spring, which in turn ensures a one-year life cycle for an individual larva. This can be seen to be beneficial to the individual, since intuitively an increase in the length of the larval (nonreproductive) stage will lead to an increase in mortality (this has not been studied explicitly as yet).

The steep ecotone found along northern edges of gaps in forests fulfill the above mentioned requirements for suitable habitat. Such gaps are relatively common in Finland, e.g. small-scale clear-cuts, forest meadows, mires and rocky outcrops. *Melampyrum pratense* is a very common and abundant species in coniferous forests, particularly pine (*Pinus sylvestris* L.) forests in Finland (Hämet-Ahti *et al.* 1986). It is a hemiparasitic and annual herb that mainly grows in places without a dense covering of other herbs. The seeds are relatively large and usually drop to the base of the parental plant (pers. obs.). Thus, even though the plant is an annual, the location of a stand of *M. pratense* is highly predictable. For an ovipositing female *E. maturna*, finding a dense stand of *M. pratense* that covers a large area will ensure adequate larval resources in the following spring. There is evidence that ovipositing females attempt to assess the amount of host plant by accepting a plant for oviposition only after they have landed several times in succession on *M. pratense* (Wahlberg 1998).

4. Distribution and population structure

Considering the habitat requirements of *E. maturna* in Finland, it is initially surprising that the species is restricted to the SE part of the country (*see* Fig. 1). Both the main host plant *M. pratense* and the forest habitat are widespread across Finland. The reason for *E. maturna*'s limited distribution appears to be linked to the historical presence of gaps in the forest. The butterfly's distribution coincides with the presence of granite bedrock at the surface of the ground (Tikkanen 1994; Fig. 2). To the east and northeast the bedrock is covered with at least 1 m of clay soils. In areas where the granite bedrock is at or close to the surface, there are naturally more rocky outcrops in the forests and the forests are drier. In contrast, in areas with a thick covering of

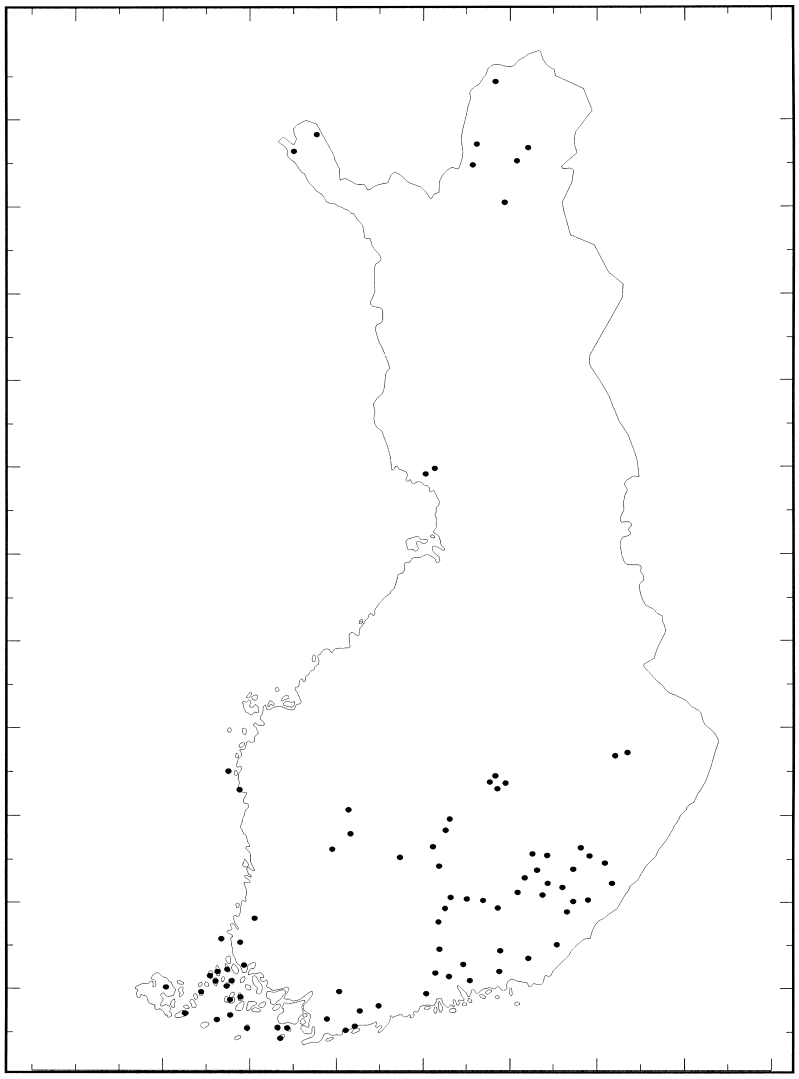

Fig. 2. The areas in Finland where the granite bedrock is at or close to the surface of the ground. The black dots represent areas where rocky outcrops are common in the landscape. Modified from Tikkanen (1994).

soil over the bedrock, the forests have been more continuous and the forests tend to be more moist. In other words, the forests in the SE have been gappier and drier than the forests elsewhere in Finland, conditions that are highly suitable for *E. maturna*.

Thus, *E. maturna* has probably existed largely in the same area it occurs in today since the species colonized Finland after the last ice age. My claim is corroborated by the observations that local populations are generally small (Selonen 1997) and therefore prone to extinction, and that individuals move short distances (Selonen 1997) and therefore can only colonize empty habitat patches that are relatively close to existing populations. These metapopulation processes (*see* Hanski 1999) are important for the long term survival of *E. maturna*. Satisfactory conditions have been present only in SE Finland, where the rocky outcrops form a dense network of suitable habitat patches. Along the edges of the surface bedrock area, suitable habitat patch networks are likely to become sparser until finally they are so sparse that extinctions of local populations are more frequent than colonizations of empty habitat patches. Another explanation may be associated with the history of land use over the past few centuries. SW Finland has mainly been under intensive agricul-

ture, while slash-and-burn agriculture was the norm in SE Finland up until the beginning of the 20th century (Pykälä & Lappalainen 1998). The latter form of land use most likely created an ideal habitat for *E. maturna*.

Modern forestry practices have created an ideal new habitat for *E. maturna* in Finland. Forests have largely been cut by private individuals in southern Finland, leading to a patchwork of small scale clearcuts with forests of different ages adjacent. The northern edges of clearcuts in dry forests usually have abundant stands of *M. pratense* and are very warm (pers. obs.), providing *E. maturna* larvae with good conditions for development. Clearcuts also provide adult butterflies with good resources. There are more flowers in clearcuts than in the natural habitat around rocky outcrops and the lush vegetation that grows a few years after the clearcut provides males with good perching sites. It would appear that clearcuts are actually a better habitat for *E. maturna* than their natural habitat. Indeed, I have observed higher densities of larval groups in clearcuts than around rocky outcrops.

A question that requires more study is why *E. maturna* has not spread further west since the commencement of modern forestry practices. One possible explanation may be associated with the presence of the granite bedrock at the surface of the ground. Such areas have thin soils and thus regeneration of forest is slower than in areas with a thicker soil layer. One can speculate that habitat remains suitable for *E. maturna* for a longer period in SE Finland than in SW Finland. Such a scenario would explain why the species has not spread west during the past decades. The extinctions of local populations simply exceed the number of new local populations being established in areas with faster regeneration of forest.

The situation described above is not unique to *E. maturna*. It is also found in the closely related Edith's checkerspot (*Euphydryas editha* (Boisduval)) in the Sierra Nevada mountains of western USA (Thomas & Singer 1998). *Euphydryas editha* is naturally restricted to the edges of rocky outcrops in pine forests but the species has colonised adjacent clearcuts recently. In contrast to the *E. maturna*, the colonisation of the new habitat by *E. editha* is associated with a change in the host plant, as the usual host plant is unable to survive in the clearcuts (Thomas *et al.* 1996). In the case of *E. maturna*, small scale clearcuts appear to be beneficial to the long term survival of the species. Clearcuts increase the density of habitat patches in a given landscape. An increase in the density of habitat patches is thought to increase the proportion of habitat patches that are occupied by the species in any given year (Hanski 1999).

5. Conclusions

The ecology of *E. maturna* in Finland is distinctly different to the ecology of the same species elsewhere in Europe. The butterfly is found mainly on forest edges with a southern exposure, where its main host plant *Melampyrum pratense* is abundant. In Finland such habitats are common, especially in the southeastern part of the country where the bedrock is very close to the surface of the ground. Also man-made habitats are important to the survival of the species in Finland, in particular small scale clearcuts in dry coniferous forests. As forestry is one of the more important industries in Finland, it appears that *E. maturna* is not under any threat of extinction in Finland. Indeed the distribution of the species has remained stable over several decades, when many other species have declined. I have presented a number of speculations in this article on host plant use and the causes of the present distribution of *E. maturna* in Finland. I hope these speculations will stimulate further research on this most fascinating species.

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