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What can the long-term ecological monitoring of the Åland islands meadow network tell us about changes in Finnish nature?

Photo: Video screenshot / RajuLive.fi

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Human induced changes in land use and in climate are having severe impact on natural populations and communities, as evidenced by recently reported declines in insects. Quantifying change and understanding the drivers underlying these changes requires long-term systematically monitored ecological data. The occurrence and abundance of the Glanville fritillary (*Melitaea cinxia*) butterfly in the Åland islands has been monitored across the 4 000 potential habitat patches continuously since 1993. This classic metapopulation has become an ecological model system in understanding how species persist in fragmented landscape. Due to the systematic long-term survey, we are now beginning to see also how on-going changes related to climate are affecting the ecology and population dynamics of the butterfly. As many other butterflies globally and in Finland, the Glanville fritillary butterfly also shows declining population trends in the Åland islands. In addition, the metapopulation fluctuations have become more synchronous in space with especially dry and warm summers having the most negative effect on the species overall.

Importance of long-term monitoring data in assessing change

When addressing questions related to responses of natural communities and populations to ongoing human-induced climate change and habitat loss long-term ecological monitoring data is of crucial importance (Brlík et al. 2021). Without such data it is very challenging to quantify how ecological systems have changed over time, to identify drivers of these changes or to forecast future trends. With data from monitoring schemes at varying spatial and temporal scale on different taxa in both terrestrial and marine systems researchers have, for example, demonstrated shifts in geographical ranges and in phenology in response to climate change (Parmesan et al. 1999, Bellard et al. 2012, Lenoir & Svenning 2015). During the last few years terrestrial insect declines have also been reported, especially in North America and in some European regions (Van Klink et al. 2020). Especially worrisome are indications of declines of previously abundant and wide range species. Habitat loss and degradation and chemical pollution have been suggested as the main drivers of the population declines of European butterflies (e.g. Wagner 2020, Warren et al. 2021) but the underlying mechanism and connection to on-going climate change still remain relatively unknown. Long-term monitoring data of insects populations are thus crucial in filling this knowledge-gap.

A more detailed information on a group of well-studied taxa can provide us insights that will help to understand and identify causal mechanisms underlying insect declines worldwide. Butterflies are highly sensitive to changes in their environment (Dennis et al. 2003), their ecology is often well understood, and many countries have long history of monitoring their spatial occurrence and even abundance via voluntary monitoring schemes. Butterflies are thus good candidates to act as an early warning indicators to assess risk of biodiversity loss resulting from climate change (Warren et al. 2021). Many butterflies in Europe and also in Finland are shifting their ranges and phenology in response to climate change, yet many are also experiencing declining population trends (Hällfors et al. 2021, Warren et al. 2021). Understanding changes in population trends require more detailed across population level assessments.

In Finland, the systematically and continuously collected annual survey of the Åland islands' meadow network provides a dataset of unique spatial and temporal resolution (Opedal et al. 2020). This dataset includes monitoring of the Glanville fritillary butterfly Melitaea cinxia, its specialist parasitoid wasp *Cotesia melitaearum*, and the specialist fungal pathogen *Podosphaera plantaginis* infecting *Plantago lanceolata*, one of the two host plants of the butterfly. Below, I describe the monitoring data collected from the Åland islands and briefly highlight some key aspects of the research carried out in this study system over the past 30 years (for a more thorough review on the butterfly research see Niitepold & Saastamoinen 2017, Ovaskainen & Saastamoinen 2018). My focus here is on the research on the Glanville fritillary butterfly. In the end I review some of the more recent work assessing the potential impact of on-going climate change on the ecology of the butterfly in the Åland islands.

History and main fields of research

In the early 90's the late professor Ilkka Hanski was looking for an empirical model system that he could use as a natural laboratory to test the theories he had developed in relation to metapopulation biology (reviewed in Ovaskainen & Saastamoinen 2018). He settled on the Glanville fritillary butterfly that in Finland only occurs in the Åland islands archipelago. In Åland the occurrence of the butterfly is restricted to the natural meadows and pastures in which one or both of the larval host–plants, the ribwort plantain (*Plantago lanceolata*) and the spiked speedwell (*Veronica spicata*) are present. Female butterflies lay their eggs on these plants, which the larvae then feed on during their development in the summer and after breaking diapause in the following spring. In 1993, Hanski and colleagues initiated the survey, that would become one of the best known ecological model systems in studying spatial and metapopulation ecology. During the fall survey the potential habitats of the Glanville fritillary butterflies are monitored for the presence and abundance of the butterfly based on their conspicuous overwintering larval nests found at the base of the host plants (for detail see (Ojanen et al. 2013) (Fig. 1). During the following years the fall monitoring of, currently around 4 000 mead-

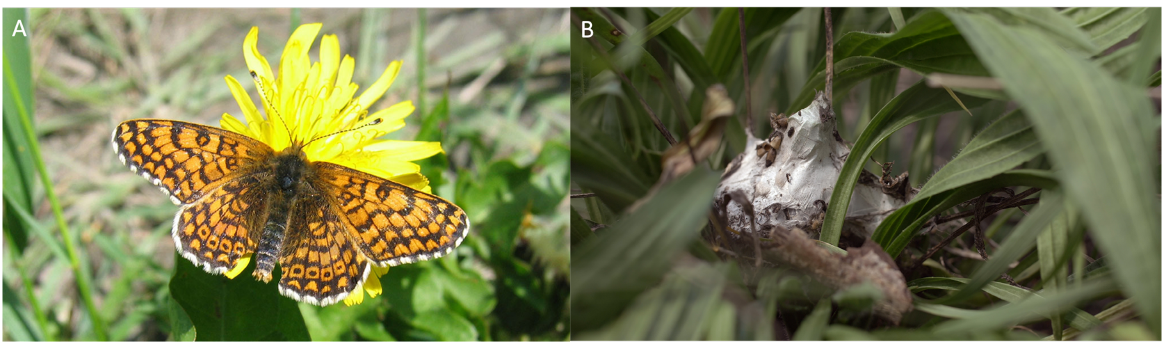

Figure 1. Adult Glanville fritillary butterfly (*Melitaea cinxia;* photo by Marjo Saastamoinen) and the larval over wintering nest (photo by Cano J. M. Arias).

ows, pastures, and even road margins, within the entire study region (50 × 70 km), became more systematic, coordinated and carried out by the students of the University of Helsinki hired as research assistants for a two week period. During the spring, the occupied habitats are revisited to assess overwintering survival of the butterfly families found during fall survey. The survey focusing on the Glanville fritillary butterfly and its host plants was soon expanded to include more community level assessment of interacting species: the occurrence of a specialized plant pathogen powdery mildew, *P. plantaginis*, of *P. lanceolata*, and presence/absence data of a specialist Hymenoptera parasitoid of *M. cinxia*, *C. melitaearum* (spring survey). The research on the plant pathogens has been seminal in assessing ecological and evolutionary questions related to disease dynamics in natural plant populations and communities (Laine et al. 2019, Numminen & Laine 2020, Susi & Laine 2020). The studies focusing on the parasitoids have demonstrated, for example, how dispersal and host range define and interact with habitat fragmentation for interacting species (reviewed in van Nouhuys 2005) and how bottlenecks influence parasitoid genetic structure and associated symbionts (Duplouy et al. 2021).

The habitat network in the Åland islands is highly fragmented and the Glanville fritillary butterfly has a classic metapopulation structure, defined by a high rate of local population turnover (local extinctions and recolonizations; Hanski 1999). The metapopulation size fluctuates greatly among years (Fig. 2). Consequently, much of the early work focused on assessing different aspects of metapopulation biology, such as impacts of spatial structure, namely patch area and connectivity (or isolation) of the habitat patches on colonization-extinction dynamics (Hanski et al. 1994), and their extensions to model more dynamic landscapes (Hanski 1999). These work provided practical tools also for conservation biology, for example assessing minimum amounts of suitable habitat requirements, extinction thresholds and viable population size (Hanski et al. 1996), metapopulation capacity (Hanski & Ovaskainen 2000), extinction debts (Hanski & Ovaskainen 2002), and so forth. The butterfly system has also been used to study how landscape structure and population processes jointly influence spatial genetic patterns (Orsini et al. 2008, Fountain et al. 2016, Fountain et al. 2018) and variation in a key life history traits, namely dispersal (Heino & Hanski 2001, Haag et al. 2005). It has also been pioneering in showing the role of inbreeding in influencing population extinction probability (Saccheri et al. 1998) and how allelic variation in candidate gene related to dispersal feed-backs to influence ecological dynamics (Hanski et al. 2017, DiLeo et al. 2018).

The land use and agricultural practices in the Åland islands are still quite traditional in comparison to the mainland Finland and most of Europe. This has most likely protected many butterflies

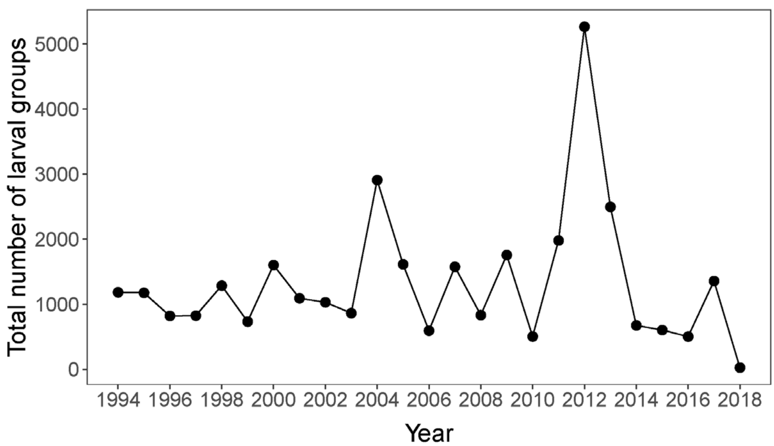

Figure 2. Changes in number of larval groups found during the fall survey 1993-2018. To correct for the minor changes in data collection among the years, data presented comes from patches that have been continuously surveyed (i.e. no missing data) since 1993.

and insects, including the Glanville fritillary butterfly, from the most common threats identified as drivers of decline, namely increased use of pesticides and loss of habitat such as traditional biotopes. Due to the absence of these more common threats, it is possible to use the system to study the impacts of climate change.

Can we see ecological changes in the Glanville fritillary butterfly over the 30-year study period due to climate change?

Changes in climatic conditions can have tremendous impacts on ectotherms directly via climate warming and changes in precipitation but also indirectly via changes in resource availability (Wagner 2020, Warren et al. 2021). In the Glanville fritillary butterfly, there is increasing evidence showing that changes in precipitation have more profound impacts than shifts in temperature, most likely due to the impact precipitation has on host plant abundance.

Based on theory, the long-term viability of a metapopulation is dependent on independent fluctuations and dynamics of its local populations (Hanski 1999). Such asynchronous dynamics alleviate fluctuations at the metapopulation level as a whole, as declining populations in some areas can be rescued from other areas with more positive population growth rates. The long term metapopulation viability can thus be compromised if spatial synchrony in population growth rates increases, for example due to changes in dispersal, predation or climate, which may all influence local population dynamics. Tack et al. (2015) used 21 years of the monitoring data from the Åland islands meadow network to analyse spatio-temporal dynamics of the butterfly. They showed two striking patterns. First, the amplitude of year-to-year fluctuations in the size of the metapopulation as a whole seemed to have increased over time. Second, they demonstrated an overall increase in the level of spatial synchrony in the population dynamics (Tack et al. 2015). In a related study, Kahilainen et al. (2018) combined longer time series of monitoring data of the butterfly with climate data for the same time period to assess whether the increased spatial synchrony in the butterfly population dynamics could be explained by an increase in synchrony of weather conditions. Results firstly highlighted that precipitation rather than thermal conditions from spring to late summer are key environmental drivers of the population dynamics, and hence associated with population growth rate of the butterfly. Furthermore, it was evident that the increase in metapopulation synchrony was paralleled by an increase in the synchrony of key weather parameters (Kahilainen et al. 2018). The study further showed that there has been no change in dispersal propensity or strength of trophic interactions with a specialist parasitoid, *C. melitaearum*, over the study period, both of which could have been alternative explanations for increased metapopulation synchrony.

It has been suggested that preferences for warm microhabitats may become maladaptive under climate change (Benton et al. 2003). The Glanville fritillary butterfly in the Åland islands lives at its northern range margin, and as an adaptation show a preference to utilize microclimatic conditions in which also higher proportion of host plants show signs of drought exposure, especially in warm and dry summers (Schulz et al. 2019, Salgado et al. 2020). Both warmer microclimatic conditions, but also feeding on mildly drought exposed host plants ensure more successful development during relatively short time window in the summer (Rosa et al. 2019, Verspagen et al. 2020, Kahilainen et al. 2022), before thermal conditions cool down in autumn and diapause is initiated. Increased larval development is beneficial because over-wintering survival seems to be higher for larger larvae (Rytteri et al. in prep), although larvae have some flexibility in when to enter diapause (i.e. 4th or 5th instar; Kahilainen et al. 2022). Salgado et al. (2020) further showed, by combining field experiments with 10 years of larval nest location and precipitation data, that the preferred drought-exposed microhabitats maximize larval nests survival in most summers. Unfortunately, female butterflies do not seem to shift habitat preference even under extreme climatic conditions such as heatwaves (Salgado et al. 2020). This mother’s choice of warmest microhabitats for oviposition that is adaptive under predominant conditions, indeed resulted in high larval mortality in the dry summer of

2018 when the plants at these sites dried out entirely. The preference for warmest microhabitats has maladaptive consequences also for the post diapause larvae under warm spring conditions, as demonstrated by Rytteri et al. (2021): Exceptionally warm weather early in the spring can cause a phenological asynchrony between butterfly larvae and their host plants. An exceptionally early and warm spring lead to larvae breaking the diapause earlier without equally advancing host plant growth, which resulted in high larval starvation. This work on the Glanville fritillary highlighted the important role of microclimatic variability within and among populations in buffering the negative impacts of warm spring conditions (Rytteri et al. 2021).

In summer 2018, Northern Europe was struck by an extreme heatwave (Bastos et al. 2020). Due to this event, we also got direct information on how such extreme conditions may impact the Glanville fritillary butterfly in the Åland islands. We combined the ecological monitoring data with climatic and satellite data to demonstrate that year 2018 indeed was an anomaly with extremely low climatic water balance values and extremely low vegetation productivity indices across the Åland islands meadow network (van Bergen et al. 2020). The population growth rates of the butterfly were strongly associated with the climatic conditions, and consequently we observed a drastic demographic decline of the butterfly, with an all-time low of only 91 larval nests being recorded during the autumn survey (van Bergen et al. 2020). Similarly, the number of occupied patches was an order of magnitude lower than in any average year (van Bergen et al. 2020). Even though based on our ecological understanding of the system, we could predict a decline in abundance, the observed decline was even more severe than anticipated by our predictions. Thus, responses of natural populations to extreme climatic events are difficult to predict even in a well-studied system. The Glanville fritillary has recovered in most parts of the Åland islands since this historical crash evidenced in 2018 (Saastamoinen, personal communication), most likely due to good enough habitat connectivity. Oliver et al. (2015) used long-term monitoring data of the British butterflies together with predictive modelling to demonstrate how the recovery of the drought-sensitive butterflies followed by a drastic decline due to extreme drought in 1995 dependent on the amount of semi-natural habitat within the landscape. However, it is becoming evident that similarly to many insects, the Glanville fritillary butterfly is also showing slight negative population trend in patch occupancy over time in the Åland islands (Opedal et al. 2020). The drivers of this negative population trend is unknown, but it is likely a combination of the changes in the climatic conditions as well as variation in host plant abundances, which fluctuate in response to climate, land use and other environmental factors (Opedal et al. 2020).

Concluding remarks

The Glanville fritillary metapopulation in the Åland islands is an ecological model system in studying spatially structured populations. The long-term monitoring data provides evidence that climate change is profoundly impacting the ecology and evolution of the butterfly by altering its dynamics and previous adaptations. In particular, the seeming lack of behavioural flexibility in habitat and oviposition site choice may result in drastic consequences if dry and warm summers and early warm springs become more frequent with climate change, which both are predicted climate change scenarios based on the recent IPCC report (IPCC 2022). Furthermore, the increased synchrony across the metapopulation may potentially increase the extinction risk of the metapopulation over time. Importantly, however, the system harbours high levels of genetic variation, increasing adaptive potential. In addition, the traditional agricultural practices in the Åland islands, at least at the moment, support good quality habitat and well-connected network, which will hopefully allow persistence of the butterfly in long-term future.

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