Niina Mattila

Ecological Traits as Determinants of Extinction Risk and Distribution Change in Lepidoptera

JYVÄSKYLÄN YLIOPISTO

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ABSTRACT

Anthropogenic threats have led to a massive worldwide loss of biodiversity. However, species are not equally at risk of extinction but species specific ecological traits determine how well the species is able to withstand threats to which it is exposed to. For successful conservation of species it is important to identify those ecological traits that predispose species to extinction risk and distribution decline. By indentifying the predisposing traits we can predict which species are most prone to decline and become threatened or even extinct. At the same time we also gain understanding of the reasons behind declines that provide a basis for proactive conservation. In this thesis, I studied three Finnish Lepidopteran taxa: noctuid moths, geometrid moths and butterflies. My aim was to determine ecological traits that predispose these taxa to extinction risk and distribution change. I also investigated ecological traits that promote range shift in butterflies. Many traits seemed to predict extinction risk and distribution change and these traits could be used in risk assessments. However, most traits that I found can be used only in national inspections because they are sensitive to climatical and environmental factors that vary between geographical locations. I suggest that from the set that I studied, only one ecological trait, larval specificity, could be used more broadly. The most widely recognized system for ranking species according to their estimated extinction risk, IUCN red list categorization system, is exclusively based on quantitative measures of populations and ignores ecological traits. I suggest that species specific ecological data should also be used to improve the accuracy of the IUCN extinction risk assessments.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I- IV. I am the first author of all papers and have contributed significantly to planning, analyses and writing of each paper.

I   Mattila, N., Kaitala, V., Komonen, A., Kotiaho, J. S. & Päivinen, J. 2006 Ecological determinants of distribution decline and risk of extinction in moths. Conservation Biology 20: 1161-1168.

II   Mattila, N., Kotiaho, J. S., Kaitala, V., Komonen, A. & Päivinen, J. 2007. Ecological causes of distribution decline and range shift in butterflies. Submitted manuscript.

III   Mattila, N., Kotiaho, J. S., Kaitala, V. & Komonen, A. 2007. The use of ecological traits in extinction risk assessments: a case study on geometrid moths. Submitted manuscript.

IV   Mattila, N., Kotiaho, J. S., Kaitala, V. & Komonen, A. 2007. Ecological traits and host plant type as predictors of distribution decline in noctuid moths. Manuscript.

1 INTRODUCTION

1.1 Assessing extinction risk for conservation

Anthropogenic disturbance, habitat loss and climate change have contributed heavily to the loss of species at rates comparable to those of past catastrophic mass extinctions (Pimm et al. 1995, Chapin et al. 2000, Thomas C. D. et al. 2004, Thomas J. A. et al. 2004). However, species are not "in the field of bullets" but species vary in their vulnerability to extinction risk (e.g. Bennet & Owens 1997, Purvis et al. 2000, Jones et al. 2003). One of the primary goals of conservation biology is to understand those mechanisms that make some species more prone than others to population decline, range contraction and extinction (Pimm et al. 1988, Caughley 1994). With this understanding, conservation managers can identify which species are at the highest risk of becoming extinct and it also helps to elucidate the nature of extinction processes and to plan conservation management.

In the absence of detailed population viability analyses, surrogate indicators are used in threatened species categorizations (O'Grady et al. 2004). Parameters commonly linked to extinction proneness are e.g. population size, range size, fragmentation of range, body size, life history specialization and temporal variability of population size (O'Grady et al. 2004). Because time and resources for collecting data on species are limited, identifying reliable and easily measured indicators of extinction risk is extremely important (Saunders et al. 1998).

1.2 IUCN extinction risk assessing system

Most countries have a legislation that obligates them to identify and protect threatened species. Various systematic protocols have been devised to assess levels of extinction risk and conservation status of species. The most widely recognized system for ranking taxa is IUCN red list that was first developed to assess extinction risk in global level (IUCN 2003). IUCN extinction risk

categorization system has acted like a cornerstone in many countries, and has increasingly been used as a tool in assessing extinction risk and conservation priorities also in national levels (Keller & Bollman 2004). IUCN extinction risk assessments are based on quantitative criteria that assign species to categories on the basis of their relative extinction risk. Criteria (A-E) are derived from wide review aimed at detecting risk factors across the broad range of organisms (IUCN 2001). Criteria require data on e.g. range size, population size, rates of decline and fragmentation of habitat. Ecological traits are not used in risk assessments but are encouraged to be taken into account in conservation management (IUCN 2003).

1.3   Ecological traits as determinants of extinction risk

Exposure to threatening processes is the ultimate cause of extinction but a species' biology determines how well it is able to withstand the threats to which it is exposed (Cardillo et al. 2004). Groups that are ecologically well known provide an excellent change to study which ecological traits make species vulnerable. However, it should be noted that correlates of species' vulnerability are often taxon and threat specific (Isaac & Cowlishaw 2004) and therefore studies should be narrowly focused on closely related, ecologically similar groups that face similar threats. Problems may arise because data are not directly available or there are correlations among ecological traits that may confound the conclusions (IV).

In some cases there are no data on population numbers, trend or distribution that are all important criteria to IUCN extinction risk assessments. However, ecology of species' may still be well known (Rassi et al. 2000). In this case we may get some information on extinction risk by using ecological traits as predictors. This is one application where ecological traits may be used (III). Knowledge of predisposing ecological traits provides also a basis for proactive conservation (Angermeier 1994) meaning that conservation can be started before it is too late. Even currently common species can have traits that make them vulnerable and keeping common species common should also be one aim in the management not just preventing the extinctions of rare ones (II). Common species' impact on ecosystem functions is probably wider than the role of already threatened species.

1.4 Trends in lepidopterans

Finnish lepidopteran fauna has been very well known due to enthusiastic amateur and more experienced lepidopterists that have reported observations and collected lepidopteran specimens for centuries (Huldén et al. 2004). There is published information on distribution available at least from period of 250 years (Huldén et al. 2004). During this period agriculture, forestry and land use have dramatically changed (Mikkola 1997, van Swaay & Warren 1999) and also climate is changing perhaps faster than ever before. At the same time when new lepidopteran species are found and spreading to Finland, some species are declining (Mikkola 1997, I, II, III). The decline has occurred more in butterflies (II) than in noctuid or geometrid moths (I, III). Decline of butterflies has been observed also across Europe (van Swaay & Warren 1999). Also range extensions northwards have been observed and this is supposed to be due to climate change (Parmesan 1996, Parmesan et al. 1999, II).

1.5 Aims of the study

For successful conservation management we should be able to predict which species are most prone to decline in the near future. This enables us to better define conservation priorities and plan management even before species begin to decline. The objective of this thesis was to identify ecological traits that predispose Finnish noctuid moths, geometrid moths and butterflies to extinction risk and distribution change. I also investigated ecological traits that promote range shift in butterflies. In addition to indentifying ecological traits that predispose to extinction risk and distribution change, the aim was also try to connect these traits to threatening factors to better understand the patterns and processes behind declines because this provides a basis for proactive management.

2 MATERIAL AND METHODS

2.1 Data

2.1.1 Distribution, distribution change and range shift

All data on distribution, distribution change and range shift was based on The Atlas of Finnish Macrolepidoptera (Huldén et al. 2000) in which the distribution of a species is given as the number of occupied 10 × 10 km grid cells in the national coordinate system. This atlas covers all reliable observations from the last 250 years. From earlier years there are only few observations, and most are from recent decades. In the atlas, distribution data are divided into observations before 1988 and observations between 1988 and 1997. The difference in these distributions (number of occupied 10 × 10 km grid cells) was used to estimate the distribution change for each species. Critique on Atlas data is discussed in paper I.

In butterflies, also the range shift was analysed (II). Range shift, i.e. the movement of the centre of the distribution for each species, is counted from the difference in the centre of the distribution between the two timescales and it is given as the distance (km) and direction (degrees) in Huldén et al. (2000).

2.1.2 Threatened and not threatened species

IUCN extinction risk categories were used to classify species as threatened and not threatened such that near threatened (NT), vulnerable (VU), endangered (EN) or critically endangered (CR) were classified as threatened and all others as not threatened. Threatened species were considered at being on the risk of extinction and species that are not threatened as not being at risk of extinction. The principal determinant of the IUCN Red List classification for lepidopterans in Finland is the area of occupancy or distribution of species (Rassi et al. 2001).

2.1.3 Species' traits, host plant distribution and other data

Data on traits were collected from several literature sources, but I also used plant distribution database (Lahti et al. 1995), data on number of observation days for butterflies (Saarinen et al. 2003) and dispersal ability data that was based on a query conducted by Komonen et al. (2004).

For noctuid (I) and geometrid (II) moths I used data on overwintering stage, larval host plant specificity, flight period length, body size and for monophagous species I used host plant distribution. In study IV I used also host plant type for noctuid moths. For butterflies (III) I had data on overwintering stage, larval host plant specificity, adult habitat specificity, dispersal ability, density, flight period length, body size and for monophagous species also host plant distribution.

2.2 Phylogeny

Statistical methods that treat species values as statistically independent data points may be problematic because closely related species share many characters through common descent rather than independent evolution (Harvey & Pagel 1991, Harvey & Purvis 1991). To overcome the non-independence of the species I compiled a likely phylogeny of noctuid and geometrid moths (Kullberg et al. 2002) and applied the method of phylogenetically independent contrasts as implemented in the CAIC software (Purvis & Rambaut 1995). However, what is not often recognized is that there are a few rather strict assumptions that must be met before the phylogenetically independent contrasts are in fact phylogenetically independent (Freckleton 2000). If these assumptions can not be met one must rely on results without phylogenetic corrections. The method of contrasts can fail e.g. if correct data transformations are not used prior to analysis (Freckleton 2000). My data could not be transformed to meet the assumptions required to achieve the phylogenetic independence in CAIC (I, III, IV). Nevertheless in the study I data was analyzed with the method of phylogenetically independent contrasts but the results were critically evaluated. Tests performed for geometrid moths were not reported. However, I may be relatively confident that my results are not biased by the phylogeny, because several studies on traits of lepidopterans have revealed that the traits under investigation are relatively independent of lepidopteran phylogeny (Lindström et al. 1994, Koh et al. 2004, Komonen et al. 2004, Päivinen et al. 2005), indicating that the investigated traits have evolved many times and independently. Moreover, uncertainties in the geometrid and noctuid moth phylogenies themself suggest that any correction based on them may be unreliable. For these reasons, I based all results on the original species' data.

2.3 Statistical tests

In an evolutionary sense I was interested in the independent effects of each of the variables and thus aimed to analyze all traits simultaneously such that the effects of other traits were controlled. However, data on traits is often insufficient and to see how single trait predicts extinction risk and distribution change in studies I, III, IV I also analyzed the effect of each trait without partialling out the correlated effects.

Statistical analyses were conducted in the SPSS program (versions 12.0 and 13.0 for Windows, SPSS, Chicago, Illinnois, U.S.A.). For phylogenetic analyses I used CAIC (Purvis & Rambaut 1995) and for the circular data I used Oriana (Kovach 2003).

3   RESULTS AND DISCUSSION

3.1   Determinants of extinction risk

I found that larval specificity is a common denominator that promotes extinction risk in noctuid moths (I), geometrid moths (III) and also in butterflies (Kotiaho et al. 2005). Species specified to only one host plant type are dependent on local abundance of host plants (Warren 1992) and because they can not switch host plants, they are more sensitive to changes. Also host plant distribution in monophagous species predicts extinction risk in all three groups (I, III, Kotiaho et al. 2005). This may be because species can not be more widely distributed than their host plants and extinction risk assessments of lepidopterans are mostly based on distribution.

Also flight period length predicts extinction risk in all three groups (I, III, Kotiaho et al. 2005). The effect on flight period on extinction risk may be because species at the edge of their distribution have shorter flight period length (Komonen et al. 2004). Species at the edge of their distribution tend to inhabit only best quality patches (Hanski 1999) and have also lower dispersal ability (Komonen et al. 2004). Limited number of suitable habitats and poor dispersal ability may be reasons that predispose species with short flight period to extinction risk.

In noctuid moths predictive traits were tested also singly without removing the correlated effects of other traits. This was done to see how single trait predicts extinction risk and if also single traits can be used as tools to estimate extinction risk if we have no data on other traits. However, I found evidence that any single trait was not enough to predict extinction risk reliably (I).

3.2 Determinants of distribution change

In noctuid and geometrid moths overwintering stage was connected to distribution change. In both groups egg overwinterers have succeeded best and this can be connected to climate change (I, III). Species overwintering as eggs are usually southern species and they commonly feed on trees (Virtanen & Neuvonen 1999). Eggs laid on trees are not covered by insulating snow cover like most pupae and larvae and are thus more prone to climatic variations and may benefit from warming climate. At the same time species overwintering under snow cover may suffer from thinning insulation or longer period without snow. In addition to these factors, egg overwinterers may benefit from warming climate because they tend to fly at late summer or autumn, time that is now extended and warmer than before (IPCC 2001).

Even though the better success of egg overwinterers can be explained with climatical factors, there may also be some other correlated traits that have effects on survival. Overwintering stage is connected to host plant type (Niemelä et al. 1982, Virtanen & Neuvonen 1999) and when the effect of host plant type was taken into account in noctuid moths, three interactions were revealed. One of the interactions was between overwintering stage and host plant type (IV). Among egg overwinterers, species feeding on trees seemed to fare the best (IV) and the fact that land use changes have affected differently on different plant types, may be one reason for unequal decline of lepidopteran species.

Measures of adult habitat specificity or dispersal ability were not available for noctuid or geometrid moths, factors that nevertheless were important determinants of distribution change in butterflies (II). It is probable that these are important factors in all groups and this should be further studied.

Flight period length was connected to distribution decline in butterflies (II) and geometrid moths (III) but as already mentioned; flight period length probably reflects some other traits that have the actual effect.

In noctuid moths (IV) and butterflies (II) larger species have declined more. It is generally assumed that large species are more sensitive to habitat fragmentation because of greater space use and food resource requirements (Cyr 2000) but this assumption ignores the fact that large species may, because of their higher mobility, be able to use multiple patches (Hambäck et al. 2007). This fact suggest that small and large species may be affected by different aspects of fragmentation: small species may be most affected by the path size reduction, whereas large species are more affected by the total amount of suitable habitat in the landscape (Hämbäck et al. 2007). Body size is connected to larval host plant specificity in geometrid and noctuid moths, more specified species being smaller (Niemelä et al. 1981, Lindström et al. 1994). This may easily lead to conclusion that smaller size predisposes to distribution decline. However, if the effect of larval specificity is removed, the result is just the opposite; larger size actually predisposes to distribution decline. These

complicated results suggest that body size is far from being a straightforward determinant of distribution change.

3.3 Why both extinction risk and distribution change?

Extinction risk and distribution change were often correlated, but this is mostly because distribution decline has been used as one criterion to estimate extinction risk. This correlation is directly reported in studies I and III: threatened species have declined more than not threatened species. Even though extinction risk and distribution decline are correlated, it seems that both should be studied: in noctuid moths (I) determinants of extinction risk did differ from those that predict distribution change. In geometrid moths predictive traits were the same (III).

Determinants of distribution change reflect more recent and ongoing threats than determinants of extinction risk because for some species, especially southern ones, extinction risk may be only theoretical due to small distribution area in our country. Based on my studies, data on both, predictors of distribution change and predictors of extinction risk are needed if we want to successfully predict which species are prone to decline and at the highest risk of extinction. Even common species with large distribution can have traits that predispose them to distribution decline.

3.4 Range shift

For butterflies, I was able to analyze traits that predict range shift (measured as the movement of the centre of the distribution) (II). Traits that were found to be connected to range shift were dispersal ability, body size and flight period length. However, methodological difficulties with data on directions and distances (circular data) prevented testing traits simultaneously to determine the independent direct effect of each trait. Thus, the results tell about the characters that are common in species that have moved along the climate but some traits may be correlated and all traits that have effects may not be shown in the analyses.

It has been observed in Britain that mobile generalist species are increasing and sedentary specialist are decreasing because they can not move along the climate (Warren 2001). This may be true also in Finland because my results show that threatened species, which often are sedentary and specialized (Kotiaho et al. 2005), have not moved to any specified direction whereas not threatened species have moved along the climate.

4 TOOLS FOR CONSERVATION

Identifying ecological traits that make some species more vulnerable than others is vital for predictive conservation science. The aim of this thesis was to determine some ecological traits that determine extinction risk and distribution change in Lepidoptera. It seems that many traits can be connected to these variables but the independent effect of each trait is not always easy to find because traits tend to be correlated and all traits may not be known. Correlations and interactions between both, traits and threatening factors complicate the task of conservationist in aims to identify predisposing traits and to understand processes behind the declines. Thus traits should be analyzed simultaneously to partial out the correlated effects and to determine the possible interaction effects between the traits.

I found several traits that predict extinction risk and distribution decline. However, only one of these, larval specificity can be used in a broader scale. Dispersal ability may also be one such trait, but unfortunately there were no data on dispersal ability of noctuid and geometrid moths. Other traits that predicted extinction risk or distribution change, e.g. overwintering stage and flight period length, were predictive most likely only because in this region the specific threat they expose to is related to harsh climate and thus they can be used only regionally.

The most widely recognized system for assessing extinction risk, IUCN red list categorization system (IUCN 2003), is exclusively based on quantitative measures of populations and ignores ecological traits even they directly contribute to the vulnerability in the first place. I suggest that taxon specific ecological data should be used to predict extinction risk to improve the accuracy of IUCN extinction risk classification.

Acknowledgements

YHTEENVETO (RÉSUMÉ IN FINNISH)

Perhosten uhanalaisuuteen vaikuttavat ekologiset piirteet

Monet ihmistoiminnan aiheuttamat muutokset, kuten elinympäristöjen tuhoutuminen ja ilmastonmuutos, ovat saaneet aikaan kuudennen sukupuuttoaallon. Lajit eivät kuitenkaan häviä sattumanvaraisesti vaan niiden ekologiset piirteet vaikuttavat siihen, kuinka hyvin ne kestävät erilaisia uhkatekijöitä. Yksi luonnonsuojelubiologian tärkeimmistä tavoitteista onkin ollut löytää ne tekijät, jotka altistavat lajit taantumiselle ja sukupuuttoriskille. Lajiryhmät, joiden ekologisista piirteistä on paljon tietoa saatavilla, antavat erinomaisen mahdollisuuden tutkia näitä altistavia piirteitä. Näiden piirteiden avulla voidaan yrittää ennustaa, mitkä lajit ovat kaikkein suurimmassa riskissä taantua tai hävitä. Kun altistavat piirteet tiedetään, voidaan suojelua suunnata hyvissä ajoin niihin lajeihin, jotka ovat vaarassa taantua. Riskien ennustaminen vaatii kuitenkin tarkkaa tietoa lajin ekologiasta, levinneisyydestä ja levinneisyyden muutoksista. Suomessa perhosten kohdalla tilanne on varsin hyvä, sillä perhoslajisto on hyvin tunnettu, ja laaja perhosharrastajajoukko on ollut innokas tallentamaan havaintojaan.

Väitöskirjatutkimuksessani pyrin selvittämään mitkä ekologiset piirteet vaikuttavat yökkösten, mittareiden ja päiväperhosten sukupuuttoriskiin ja levinneisyyden pienenemiseen Suomessa. Lisäksi tutkin päiväperhosten levinneisyyden painopisteen muutoksen suuntaan vaikuttavia ekologisia piirteitä. Yritin myös selvittää, mitkä uhkatekijät voidaan yhdistää levinneisyyden muutoksille ja sukupuuttoriskille altistaviin ekologisiin piirteisiin.

Tutkimukseni osoitti, että piirteet tulee analysoida yhtäaikaisesti samassa mallissa, jotta piirteiden riippumaton vaikutus ja mahdolliset yhdysvaikutukset tulevat esille. Löysin monia piirteitä, joiden avulla sukupuuttoriskiä ja levinneisyyden pienenemistä voidaan ennustaa, mutta suurinta osaa näistä piirteistä voidaan käyttää riskinarviointiin vain Suomessa, sillä ne riippuvat ympäristötekijöistä kuten ilmastosta. Näyttäisi kuitenkin siltä, että erikoistuneisuus ravintokasviin toukkavaiheessa altistaa lajin sukupuuttoriskille huolimatta ympäristötekijöistä, ja sitä voitaisiin käyttää yhtenä kriteerinä perhosten uhanalaisuusluokituksissa ympäri maailman. Nykyinen yhä yleisemmin käytetty IUCN:n (Maailman luonnonsuojeluliiton) uhanalaisuusluokitus perustuu vain määrällisille muuttujille, kuten lajin populaatiokoolle ja levinneisyydelle tai näiden muutoksille, eikä lajien ekologisia piirteitä oteta mukaan arviointeihin vaikka niillä on kiistaton vaikutus.

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