Empirical and Theoretical Studies of Population Trends and Extinction Risks

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Abstract

Empirical and theoretical approaches are needed to solve the current problem of increased extinction risk for many species. Thus, this thesis focuses on: (1) ways to estimate population trends for a large number of species, and (2) a predictive framework for identifying vulnerable populations from species traits or life history traits to allow for more proactive conservation actions. I estimated long-term population trends and range-abundance dynamics of longhorn beetles using Natural History Collections. In general, negative population trends were not accompanied by declines in range, but range increased among species with increasing populations. The analysis also exemplified how the results can be used in the red listing process. Linking life history traits and two metrics of extinction risk (population trend and red list classification) in long horn beetles showed that generation time, overwintering stage, larval host plant specialisation, adult activity period and body size were related to extinction risk, often with interaction effects between predictor variables.

Variability in population size is an important factor affecting population extinction risk. I modelled the effects of demographic and environmental stochasticity on extinction risk in small populations, for a large range of life history types. Extinction risk due to demographic stochasticity increased with increasing fecundity and decreasing age of maturation, whereas effects of adult survival interacted with maturation age. Including environmental stochasticity showed that the qualitative relationship between extinction risk and life history types changed, but also that combined effects of both stochasticities on extinction risk were most significant in short-lived life histories.

The results suggest that data from Natural History Collections can be used to estimate long-term population trends, and that population declines may be underestimated if estimated from changes in range. My studies also suggest that life history traits and species traits can be used to predict population vulnerability to extinction and, hence, that certain groups of species are more vulnerable to extinction than others.

Keywords: Population dynamics, Extinction, Life history, Population trends, Rarity, Demographic traits, Cerambycidae, Conservation biology

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Dedication

Till mina föräldrar och till Linda för att ni, mer eller mindre medvetet, gjort mig till den jag är.

Always start out as simple as possible, as things turn out complicated enough in the end either way

Pär Forslund (freely translated)

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Jeppsson, T., Lindhe, A., Gärdenfors, U., Forslund, P. 2010. The use of historical collections to estimate population trends: a case study using Swedish longhorn beetles (Coleoptera: Cerambycidae). Accepted for publication by *Biological Conservation*.

II Jeppsson, T., Forslund, P. Factors explaining species differences in Red list status and long-term population trends in longhorn beetles – a comparative study (manuscript).

III Jeppsson, T., Forslund, P. Can life history type predict the effect of demographic stochasticity on extinction risk? (manuscript).

IV Forslund, P., Jeppsson, T., Pärt, T. Life history related effects of environmental and demographic stochasticity on extinction risk (manuscript).

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Introduction

We are currently in what has been called a species extinction crisis (Ceballos & Ehrlich, 2002; Purvis *et al.*, 2000c; Balmford, 1996). Conservation biology aims to understand the underlying reasons for the loss of biodiversity, and to guide conservation practice. Therefore, understanding the patterns and dynamics of species extinction is essential if we are to (1) categorise species according to risk and (2) understand why some species are more threatened by extinction than others. The first point is important both as a description of the current situation and for effective resource allocation in conservation activities. The second point is necessary for the development of an explanatory and/or predictive framework for conservation biology (Purvis *et al.*, 2000c). The preservation of biodiversity can be justified on several grounds, but it is a fact that loss of biodiversity will make ecosystems less robust, less complex and may trigger cascading effects that we often cannot oversee the consequences of (Brook *et al.*, 2008). Ecosystem functioning will also be strongly affected by biodiversity loss (Hooper *et al.*, 2005; Luck *et al.*, 2003; Loreau *et al.*, 2001)

Because of the multiple tasks that face conservation biology, different types on knowledge are needed to guide practice. An overarching issue is the lack of species specific knowledge, and many species are not described, only known by name, and/or known rather rudimentary. Therefore, generalised knowledge on extinction dynamics is essential for successful large scale species conservation. The most basic information needed to assess the extinction risk of a population is its size and spatial distribution. With information over time we can estimate a population trend, and paper I address this problem in the face of sparse data. Information on species traits can be used to differentiate levels of threat based on e.g. trophic level, longevity, dispersal ability etc. To this end, paper II analyse how the current patterns of extinction risk and population trends are associated with life

history traits in long horn beetles. The life history of species affects the influence that general factors such as fragmentation, environmental variability and demographic stochasticity will have on population dynamics. Paper III and IV therefore study some aspects of population dynamics in small populations in relation to common life history traits.

Background

This thesis is written from the perspective of single population dynamics, i.e. not focusing on species interactions, community ecology or landscape ecology. The background section covers aspects that I feel are important for understanding the results presented here, and the overall approach of this thesis.

(Some of) The challenges for conservation biology

Conservation biology is essentially an applied subject. At the same time the subject can be found at the crossroads between applied and basic research, in the sense that both approaches are needed to understand what is happening in threatened populations or ecosystems. Several rather distinct activities can also be discerned within conservation biology. Caswell (2001) separate (as an analogy to medicine) (1) Assessment, (2) Diagnosis, (3) Prescription and (4) Prognosis, as aspects and problems in need of different methodologies. Assessment is naturally the first step when looking at the status of a species, and can include either metrics of population health (such as extinction risk or stochastic population growth rate) or species traits (predisposing some species to vulnerability of population extinction). Diagnosis deals with identifying the specific causes for why a population is threatened (e.g. life table response experiments in structured population models), Prescription with the most affective management actions (Prospective analysis - Caswell, 2000), while Prognosis deals with projections of population fates (e.g. Population viability analysis – Morris & Doak, 2002; Beissinger & McCullough, 2002; Sjögren-Gulve & Hanski, 2000; Gilpin & Soulé, 1986).

The magnitude of the biodiversity crisis means that actions in conservation biology must be based on generalised knowledge at the species

level, or on conservation measures on a higher level than species (e.g. ecosystems or habitat conservation). We do not have, and will never have, specific knowledge on all species where conservation action is needed. The problem is especially pressing in small populations, where the accurate estimation of parameters relevant to assess population health, and diagnose the reason for why the population is threatened, is often practically impossible. Therefore, generalised patterns and rules of thumb are necessary to guide practical conservation, at least until better knowledge is at hand.

The work presented in this thesis mainly deals with aspects of assessment of species extinction risk, either through estimation of population trends (I), by establishing how species traits are related to population changes and extinction risk (II), or through theoretical models of extinction risk for generalised life history types (III & IV).

Population models

The use of population models can be divided into two broad categories. The first type of models aims to describe the dynamics of specific populations as accurately as possible, given the available data. In respect to models in conservation biology, population viability analysis (PVA) is an example of this approach (Beissinger & McCullough, 2002). The second type of modelling approach aims to use models to study how general demographic factors influence the population dynamics of different types of species. This is done by exploring model dynamics over a range of relevant parameters values, and the explicit goal is to understand how the modelled factors affect different types of populations. The division between these two approaches is not razor sharp, and mainly serve to show the distinction between two general reasons for using models - the former has a very specific applied goal, while the latter strive for general, but unspecific, understanding of processes.

Variability enters population models mainly in two ways – through environmental variability and due to variability in the fates of individuals. These two sources are termed environmental stochasticity and demographic stochasticity. Spatial variability in the environment (environmental heterogeneity) is sometimes included in environmental stochasticity, but in this thesis only environmental variability over time is considered. Since the sources of environmental variation are often unknown, we cannot predict environmental states over time with certainty, and this introduces randomness to models. Therefore, probabilistic statements are often needed when studying population dynamics, and extinction risk is an intrinsically

probabilistic concept (individual populations go extinct or not). It is important to remember that 'the environment' can represent different things in different models, depending on boundary conditions, so e.g. the effects of climatic variability and species interactions can both be represented by this term. Demographic stochasticity is mostly an issue for small populations, due to the law of large numbers, but since conservation biology often deals with small populations this factor cannot be ignored. Two sources of demographic stochasticity has been identified, the effect of individual fates from probabilistic models (think coin tosses) and individual variability (also termed individual heterogeneity) (Fox, 2005; Kendall & Fox, 2002). In my mind it is unfortunate that these two concepts are discussed under the same heading, since they are connected to diametrically opposite forces; the former essentially expresses lack of knowledge, while the latter describes the effect of known variability. To put it another way; the probabilistic nature of demographic stochasticity is caused when we assign individuals to categories and use average rates to describe the category (i.e. are ignoring variation) and the effects from individual heterogeneity are created when we measure and describe the individual variability within categories. This confusion has also been touched upon elsewhere (Melbourne & Hastings, 2008). In this thesis I am only dealing with demographic stochasticity in the first sense.

The modelling of extinction risk of general life histories can utilise several approaches. Unstructured models have been used to study the effects of population growth rate, temporal correlation in environmental variability, and density dependence (e.g. Cuddington & Yodzis, 1999; Gabriel & Burger, 1992; Leigh, 1981). To capture the inherent demographic structure of naturally occurring populations structured models are used (i.e. models that divide individuals into several classes). This allows for other aspects of population dynamics to be studied, e.g. the differential effects of correlated environmental variation in annual and perennial life history types (Heino & Sabadell, 2003), the effects of demographic stochasticity in complex life histories (Legendre *et al.*, 1999; Kokko & Ebenhard, 1996), or the sensitivity of population growth rate to changes in vital rates (Brault & Caswell, 1993). However, while allowing more accurate modelling of life histories, structured models require additional data to be parameterised. For general results to be widely relevant for conservation biology they must be based on rather simple models, since they will otherwise not be applicable for the majority of species. In this thesis I used matrix models with four demographic parameters, which allow characterisation of life history types along important life history dimensions,

while being simple enough that parameter estimates are available for many natural populations (either explicitly estimated or by crude approximation).

Determinants of extinction risk

There are many causes for species extinctions, acting at different explanatory levels. Four main ultimate causes of species extinction have been identified on a global level, responsible for most current species extinctions or declines (Caughley, 1994; Diamond, 1984). These are (1) excessive hunting, (2) habitat loss or fragmentation, (3) introduced species, and (4) coupled extinctions. To these we can also add (5) pollution and (6) climate change (Thuiller, 2007; Millennium Ecosystem Assessment, 2005). All these causes are due to human-induced changes in the living environments of populations, and to attack these issues to lessen their impact are at the heart of conservation biology. These ultimate factors must be dealt with to stop the rapid loss of biodiversity, but offer little guidance to which species are threatened by extinction, and gives little help in how to prioritize between species.

There are a number of empirical and model based populations-level generalisations that describe differential risk of extinction between species, e.g. that extinction risk increase with small population size, small geographical range, increased fragmentation of populations, small sub-populations, and high rates of population decline (e.g. Mace *et al.*, 2008; Purvis *et al.*, 2000b; Noss, 1999). The process of species red listing (IUCN, 2010) relies heavily on these results, and all factors mentioned above represent strong symptoms of extinction risk.

These population level traits do, however, little to explain why some species are more threatened by extinction than others. Therefore, they have little value in a framework for predicting species differences in extinction risk, but can work well for quantifying current levels of risk. However, even then, static views on how e.g. species density is related to extinction risk does not take factors such as natural vs. man-made rarity into account, something that affects how well populations cope with low population density or increased levels of fragmentation (Henle *et al.*, 2004). Species extinction is highly non-random process (Purvis *et al.*, 2000a), affecting some taxa more than others. This implies that closely related species share traits making them more or less prone to extinction, as compared to other species. This observation led to the realisation that a proactive conservation biology could be constructed by establishing how species traits (in the widest sense of the word) are connected to increased levels of extinction

risk (Reynolds, 2003). Then, by applying the relationships that have been found, species could be divided into categories of extinction risk based on their individual species traits. Ideally, such a framework could pinpoint the most "extinction prone" species, so that conservationists would not only rely on identifying threatened species on after-the-fact quantitative population traits (such as small population size), but also put effort to prevent the most extinction prone species from becoming threatened in the first place. This idea is what has fuelled the application of comparative methods in conservation biology (Fisher & Owens, 2004; Purvis *et al.*, 2000c), and several studies have been performed, covering diverse taxa, with the aim of uncovering robust general relationships (e.g. Nylin & Bergström, 2009; Mattila *et al.*, 2008; Cardillo *et al.*, 2005; Kotiaho *et al.*, 2005; Jones *et al.*, 2003; Owens & Bennett, 2000; Purvis *et al.*, 2000b).

While such a tool for assessing species is a very attractive concept, application has shown that simple generalisations are elusive. There are two main reasons for this. First, there are many sources of population threats (e.g. see the main ultimate causes above), and different species traits are related to different sources of threat (e.g. Isaac & Cowlishaw, 2004; Owens & Bennett, 2000). This problem can potentially be overcome by looking at predictors for different sources of population threats separately. Second, the relationships between species traits and extinction risks often differ between species groups (Purvis *et al.*, 2000c). This has two consequences; (1) that established relationships between extinction risk and species traits in one group of species cannot be readily generalised to other taxa, and (2) that large-scale studies covering several taxa might fail to detect relationships that are present within narrower groups of species (Fisher & Owens, 2004). Another fact that complicates simple generalization from comparative studies is that traits never act in isolation, but often interact in the shaping of extinction risk. For instance, habitat preferences interacts with the effect of litter size in Australian mammals (Cardillo, 2003), and multiple interactions between species traits explained distribution changes in Finnish moths (Mattila *et al.*, 2009). Nevertheless, comparative studies have strengthened conservation biology by uncoverering previously unknown relationships (Fisher & Owens, 2004) and can be used to test theoretically derived hypothesis (Reed & Shine, 2002).

Another avenue to attain predictions about species extinction risk is through theoretical populations models. These have e.g. been used to investigate the effect of stochastic factors on population dynamics and extinction risk (Lande *et al.*, 2003), and to examine the relative sensitivity of life histories to changes in demographic traits (Caswell, 2001).

Environmental stochasticity represents the effect on population growth rate that is due to variability of the environment. Due to the multiplicative nature of population growth, stochastic population growth rate decrease, and hence extinction risk increase, at higher levels of environmental variability (Lande *et al.*, 2003; Tuljapurkar, 1982). Tuljapurkar (1982) also showed how the stochastic population growth rate relates to individual demographic traits, such that species differ in their sensitivity to variability in demographic traits. As a consequence, semelparous "fast" life history types are sensitive to changes in juvenile survival and development time, while iteroparous, "slow" life histories are sensitive to variation in adult survival (e.g. Jonsson & Ebenman, 2001). Environmental variability can be either uncorrelated (white) or correlated (coloured) (Vasseur & Yodzis, 2004; Pimm & Redfearn, 1988). Red-coloured noise, for example, means that environmental conditions in consecutive years are positively correlated (good and bad years come in clusters), whereas white-coloured noise refers to completely random environmental conditions each year (Halley & Kunin, 1999; Halley, 1996; Pimm & Redfearn, 1988), and the type of temporal correlation will influence how variability affects the extinction risk of species (Schwager *et al.*, 2006; Petchey *et al.*, 1997; Lawton, 1988). The effect of noise colour also interacts with species' life history type, such that extinction risk of iteroparous life history types increase in coloured environments, while it decrease in annual species (Heino & Sabadell, 2003). The amount and correlation structure of environmental variability also interacts with the type of density dependence (Schwager *et al.*, 2006; Petchey, 2000; Cuddington & Yodzis, 1999). It should also be pointed out that the inclusion and modelling of density dependence will strongly affect model dynamics and population extinction risk, especially so for structured population models (Benton *et al.*, 2006; Sabo *et al.*, 2004). An evolutionary interpretation of Tuljapurkar's approximation (Tuljapurkar, 1982) reveal that species should exhibit lower variability in the vital rates for which their population growth rate is most sensitive, since population growth rate can be interpreted as population fitness (Morris & Doak, 2004; Pfister, 1998). This means that there should be an empirical pattern of negative correlations between variability and sensitivity.

In contrast to a deterministic view, populations may go extinct due to the randomness in individual fates (demographic stochasticity), and this will cause the stochastic population growth rate to decrease in small populations. The effect of demographic stochasticity is stronger in small populations, and the effect scale as a negative exponential to population size (Lande, 1993). Early studies suggested that demographic stochasticity could be all but

ignored for populations larger than 100 (e.g. Shaffer, 1987; Leigh, 1981; Richter-Dyn & Goel, 1972), but more explicit modelling of structured populations showed that the strength of demographic stochasticity interacts with the life history of species and can be relevant for even larger populations (Fujiwara, 2007; Kokko *et al.*, 1998; Kokko & Ebenhard, 1996; Gilpin, 1992; Mode & Pickens, 1986). Hence, the effects of demographic stochasticity are larger in life histories with high fecundity (Kokko & Ebenhard, 1996; Gilpin, 1992) and the effect of delayed reproduction interacts with fecundity (Kokko & Ebenhard, 1996). The strength of demographic stochasticity is also influenced by social structure and breeding system (e.g. Gabriel & Ferrière, 2004; Legendre *et al.*, 1999). Lande (1998) showed how the combined effects of environmental and demographical stochasticity produce an unstable equilibrium population size, under which populations tend to extinction. This is essentially a description of the R-vortex of population extinction postulated by Gilpin & Soulé (1986), and the effect on populations growth will from a practical viewpoint be similar to an Allee effect (Lande *et al.*, 2003; Stephens *et al.*, 1999; Lande, 1998; Allee *et al.*, 1949). However, since demographic variance differs between species depending on life history, the unstable equilibrium will be found at varying population sizes. To summarize; there is much evidence that the effect of demographic stochasticity differs between life history types, and that the amount of demographic variance is structured by demographic traits (Saether *et al.*, 2004). Even so, there is a lack of general knowledge on how the effects of demographic stochasticity scale with demographic traits in the fast-slow spectrum of life histories, e.g. fecundity, adult survival and maturation age. I deal with this question in paper III.

Aims & motivations

The overarching aim of this thesis is to use broad comparisons across species to inform conservation biology and increase the knowledge on population dynamics of threatened species. For this goal I use both empirical and theoretical approaches. The thesis includes several types of problems from the field of conservation biology.

More specifically, I tackle three subject areas; (1) estimation of species trends for species with sparse data (I), (2) the connection between species traits and estimated extinction risk (II), and (3) theoretical modelling of species life history types to evaluate how stochasticity influence their extinction risks (III and IV).

Paper I

Systematically collected population data that allow estimation of species trends is hard and expensive to gather, for most species. However, records of species encounters have been gathered by museums and amateurs over the years and are assembled in Natural history collections (NHCs). The question is how valuable are such non-systematic data for estimating changes in population trends and species distributions? In paper I, we analysed long-term NHC records of long horn beetles in Sweden, with the aim of estimating population trends, and to distinguish between different processes of population change. Since this type of species information is available for most species groups, the methodology can potentially be an important tool in the assessment of species for red listing (criterion A).

Paper II

Comparative studies that connect species traits to extinction risk are an important tool in conservation biology. In paper II, we analyse long-term trends and red list classification of Swedish long-horn beetles to: test whether ecological and demographic predictors of extinction risk, such as food specialization, body size and longevity, can explain variation in the two above mentioned proxies of extinction risk in Swedish longhorn beetles. As these two metrics of extinction risk are connected to different sources of population extinction risk - trends to population decline and red list classification to small population size - we also tested whether species traits were only linked to one or both metrics of extinction risk.

Paper III

Demographic stochasticity is an important factor in determining the extinction risk of small populations, but there is a lack of general knowledge on how life history types interacts with demographic stochasticity. In paper III, we explore how demographic stochasticity affects the extinction risk of generalised life history types, especially whether certain life history types are more affected by demographic stochasticity than others, and how demographic traits are related to extinction risk.

Paper IV

Paper IV aims to extend the theoretical analysis from Paper III to include the environmental stochasticity, both as a single factor and in concert with demographic stochasticity. Our twin goals are to; (1) see if the qualitative relationships between demographic traits and extinction risk hold in the extended model; (2) test how these two stochasticities interact across life history types, and if certain life history types are more vulnerable for the combined effects of demographic and environmental stochasticity than are others. We study these effects at different levels of environmental variability to assess how robust the results are.

Methods

Longhorn beetles in Sweden (I & II)

About 117 species of longhorn beetles (Coleoptera: Cerambycidae) have been found naturally occurring in Sweden, and out of these 50 are currently red listed (Gärdenfors, 2005). They generally have a long larval stage, stretching over one to several years, and a relatively short adult stage where they reproduce(Ehnström & Holmer, 2007). Most species are saproxylic, i.e. are dependent on dead wood for their development and survival, but some utilise living or weakened woody plants or herbs. It is a relatively well known insect group, which means that the biology and distribution of species is often well known. Their large size and appearance have made them popular among entomologists and many records of species encounters are now in museums, private collections and printed publications such as entomological journals (Lindhe *et al.*, 2010).

The generation times of longhorn beetles in Sweden range between one to five years, and no species produces several generations per year. There is also a large diversity in other life history traits and ecological traits, such as body size, habitat choice, substrate classes used, degree of substrate specialization, modes of overwintering, and phenology. Because of changes in human land use, both forest and agricultural landscapes (Axelsson *et al.*, 2002; Siitonen, 2001; Linder & Ostlund, 1998; Ihse, 1995), many species of longhorn beetles are thought to be in decline (Ehnström & Holmer, 2007). Several species are also considered threatened due to small and geographically restricted populations (Gärdenfors, 2005). There is a lack of knowledge on why some species are more threatened than others, and how the variation is explained by species biology.

Population trends of longhorn beetles (I)

A database compiling records of longhorn beetle encounters was assembled during 2000 – 2008, and the database includes records from early 18th century to present time. In the analysis presented here we focused only on the 20th century (for longer timeframes see Lindhe *et al.*, 2010). Each records gathers information on the species identity, location, encounter date and the name of the collector, along with other information. The records represent both physical specimens from museums or private collections, information from the literature and oral reports from the Swedish Species Information Centre (ArtDatabanken), but the vast majority are of the first category. A full account of the database can be found in Lindhe et al. (2010). Biological information of this type is labelled Natural History Collections (NHCs) and has been receiving increased levels of interest (Silvertown, 2009; Lutolf *et al.*, 2006; McCarthy, 1998; Burgman *et al.*, 1995), probably due to their vast range of possible application and the general lack of long-term information on species abundance and range for most species. Analyses of NHCs have been used to estimate changes in abundance, range or biodiversity (e.g. Duffy *et al.*, 2009; Grixti *et al.*, 2009; Kotze *et al.*, 2003; Hedenäs *et al.*, 2002; Ponder *et al.*, 2001).

The numbers of yearly records of a particular species in our database vary depending on the abundance of the species, but also due to the sampling intensity exerted by active beetle collectors. This latter factor must be accounted for, and we used the total number of species records of non-red listed species over time as an estimate of temporal sampling effort. The estimate of sampling effort was then used to offset the yearly number of species' records to calculate a Population Size Index (PSI) as:

$$Population\ size\ index\ = \frac{Number\ of\ species'\ records}{Sampling\ effort}$$

It was also apparent that the overall frequency of red listed species was increasing over time, so this group of species was treated separately. A Gompertz function was fitted to describe the change in frequency, and this was used to adjust the yearly estimate of sampling effort for the group of red listed species. The estimate of sampling intensity for each species was restricted to the geographical region the species had been found in. Estimates of species range over time, which takes spatial sampling intensity into account, was calculated both for fixed time periods and by using a moving window over time. This information was used to estimate species

trends over 30 and 60 year periods, using generalized linear models. A continuous generalized linear mixed model was used to test if time, range and the number of collector explained the changes in the Population size index, and we also evaluated if population trends were explained by species rarity, and if this differed between increasing and decreasing species.

Comparative study between species traits and metrics of extinction risk (II)

To assess the effect of how species traits influence extinction risk in longhorn beetles in Sweden we analysed a number of traits against two proxy metrics of population extinction risk – the Swedish red list classification (Gärdenfors, 2005) and long-term population trends (see Paper I). The analysis was performed with generalized linear models, in a multiple regression framework. We analysed the effect of the species traits body size, generation time, number of larval host plants, egg count, decomposition stage of the wood used by larvae (early vs. late), adult activity period, overwintering stage before reproduction and substrate utilization breath.

In a statistical analysis, species cannot apriori be viewed as independent entities since they share an evolutionary history (Freckleton, 2009; Felsenstein, 1985), and this must be taken into account. We used the phylogenetic regression (Grafen, 1992; Grafen, 1989) to test for phylogenetic patterning in our response variables, but none were found, so we present the simpler analysis that exclude phylogeny.

Modelling of general life history types (III & IV)

To model general life history types we have used a simplified version of partial life cycle analysis (Oli, 2003; Caswell, 2001; Oli & Zinner, 2001). The model contains four parameters; fecundity (m), adult survival (P_a), juvenile survival (P_j) and age of maturation (α). Age of maturation determined the number of juvenile stages in the model. The model is described by:

$$A = \begin{bmatrix} 0 & 0 & \dots & F_j & F_a \\ P_j & 0 & \dots & 0 & 0 \\ 0 & P_j & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & P_j & P_a \end{bmatrix}, \quad N_{t+1} = AN_t$$

We modelled a post breeding census, so the fertility terms $F_x = P_x \star m$. This is a simple matrix model that is constructed from basic demographic data that is obtainable, or at least possible to approximate, for a large number of species. Our model excludes effects of breeding system (Gabriel & Ferrière, 2004; Legendre *et al.*, 1999; Gabriel & Burger, 1992) and density dependence. Since the deterministic growth of a population is the main determinant of extinction risk, population growth must be standardised between life history types. We did this by setting three of the parameters in the model – α, P_a and m – and adjusting P_j to fix the deterministic population growth (lambda) of A to unity.

Life history types were generated by exploring the parameter ranges f: 1–15, Pa: 0.1–0.9, α: 1–10. This allowed us to study life history spectra of early-late reproduction, iteroparous-semelparous survival patterns, few-many offspring, and ore generally a range between "slow" and "fast" species life histories (Dobson & Oli, 2007; Saether *et al.*, 2004).

Extinction risk due to demographic stochasticity (III)

To calculate analytical extinction risk due to demographic stochasticity we used multitype branching processes (e.g. Caswell, 2001). We assumed the binomial distribution for survival and the poisson distribution for fecundity, distributions commonly used when modelling these traits (Morris & Doak, 2002). We calculated extinction risks over 100 years.

To further explore differences in extinction risks between life history types we calculated demographic variance, using the methods of Engen et al. (2005). This allowed us to view decompose demographic variance into contributions from matrix entries. It has been suggested that demographic stochasticity can be ignored for population sizes under 100 individuals (Mace *et al.*, 2008; Shaffer, 1987), even though studies have shown that this is not the case (Kokko & Ebenhard, 1996; Gilpin, 1992). To evaluate this hypothesis we also calculated practical population threshold levels needed to meet an extinction risk criteria of 5% over 100 years.

Extinction risk in models including demographic stochasticity and environmental stochasticity (IV)

To assess if the patterns found in paper III hold when including environmental variation, we performed a simulation study of extinction risk using the same basic model. This allowed us to introduce different levels of environmental variability, and to realistically study the extinction dynamics given our assumptions. The parameter values used in simulations were:

fecundity (m)=[1, 5, 10], adult survival (P_a)=[0.10, 0.50, 0.75, 0.90], age of maturation=[1, 2, 7]. We studied extinction risks at three levels of environmental variation, and used the same assumptions for demographic stochasticity and the same timeframe as in paper III.

Environmental variation was generated by simulating time-specific demographic parameters by using the stretched beta distribution, and uncorrelated values was obtained my using the methods of Morris & Doak (2002). These demographic parameters were then used to build time-specific transition matrices. We used 1000 simulation replicates to calculate extinction risks for each life history type.

Results & discussion

Population trends of longhorn beetles, and how they interact with the range and commonness of species (I)

Populations may change in size as a result of changed density and/or changed spatial distribution (range). We found similar patterns of population size changes between red listed and non-red listed species, with similar changes over both over longer and shorter time frames, so the distribution of population changes did not seem to depend on species rarity. However, changes in population size (measured by the *Population size index*) were more closely related to range for rare species than in common species. The relationship to range also differed between increasing and decreasing species.

We did not observe range declines in declining species, irrespectively of commonness, while in increasing species the range increased among rare but not common species (Fig. 1). This indicates that decreasing species are facing a population thinning. The result also implies that population declines could go undetected if change in population range is used as a metric of population change, as is sometimes the case. For instance, the IUCN red list allows for range to be used as a metric of population change in lack of other estimates of population trend (Gärdenfors, 2005). However, our observation that population declines could go undetected may be dependent on the scale of our study.

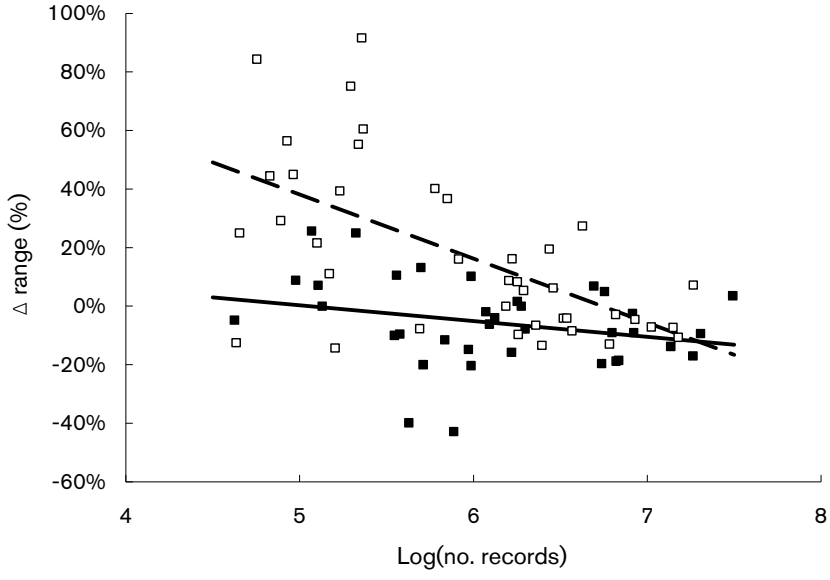

Figure 1. The relationship between the change in relative species range and log(number of records) for increasing (open squares and dashed line) and decreasing species (closed squares and solid line). Higher values of log(no. records) represents more common species.

In declining species, we expected that rare species would show larger range contractions than common ones (Hanski & Gaggiotti, 2004), but this was not the case. Possible explanations to our result is that population density have declined, maybe due to deteriorating habitat quality, or that range contraction is taking place at a smaller spatial scale than used in our study, and hence scattered. To evaluate these results further and test these explanations more knowledge is needed, more specifically on how global and local rarity is related (Brown *et al.*, 1995), and patterns of population decline at finer spatial scales.

In increasing species, rare species showed larger range expansions than common species. This suggests that common species occupy most suitable habitat, while rare species occupy suitable existing but vacant areas when populations increase (Freckleton *et al.*, 2005; Holt *et al.*, 1997).

We find that, based on this analysis, 14 species in our dataset should potentially be red listed, and only 4 of these are currently red listed (based on criteria B – geographical range). Thus our analysis can be used as a complement to the ordinary red listing process. It should be pointed out that due to our treatment of the data, and the fact that local population size is not taken into account, both estimated increases and declines are likely to

be underestimations of the real changes taking place. However, the limitations of the data must be kept in mind (e.g. not being absolute counts of population size). We also stress that the population estimates are in relation to an estimate of sampling effort, and relative to the overall trend of longhorn beetles in Sweden.

The relation between species traits and extinction risk in longhorn beetles (II)

We analysed how life history traits and ecological traits are related to two metrics of extinction risk; long-term population trends and red list classification. Our analysis of long-term population trends showed that adult activity period, generation time and overwintering stage explained the observed trends (Table 1). We also found a significant interaction between generation time and overwintering stage, showing that the negative relation between generation time and population trend was only observed in species overwintering as larvae (Fig 2).

Table 1. *Results for final multivariate models after model reduction. The table only includes factors included in the final models. For overwintering stage larvae is used as reference, so the effect shows how species that overwinters as adults differ from those that overwinter as larvae. The same is true for the interaction effects including overwintering stage, so the table shows how the slope of explanatory factors differ between adult and larval overwinterers.*

	Red list		**Long-term trend**	
Trait	**est. (st.err)**	**p-value**	**est. (st.err)**	**p-value**
Adult activity period	0.012 (0.009)	0.163	0.007 (0.003)	0.011
Body size	0.582(0.505)	0.250		
Generation time			-0.391 (0.108)	0.000
Larval host plants	3.07 (0.94)	0.001		
Overwintering stage adults vs. Larvae	3.22 (3.55)	0.365	-2.63 (0.80)	0.001
Adult activity period * overwintering stage	0.053 (0.021)	0.011		
Body size * overwintering stage	-3.20 (1.23)	0.009		
Generation time * overwintering stage			0.824 (0.298)	0.006
Larval host plants * adult activity period	0.027 (0.011)	0.017		
Nagelkerke R^2 (%)	29.0%		27.3%	
n	105		77	

When analysing which traits that were related to the red list classification we found that the degree of larval plant specialisation along with several interaction factors explained species differences. Specialised species were found in higher red list classes (i.e. are more threatened), and this trait also had a positive interaction with adult activity period. Among species overwintering as adults, species with long adult activity periods were more likely to be classified as less threaten than those with short activity periods. Overwintering stage also interacted with body size, so that species of large size that overwinter as adults were found in higher red list classes. Our models explained between 27 - 29% of the variation in the response variables.

We found that different species traits explained extinction risks, depending on the source of population threats. Therefore, our results suggested that relationships between species traits and extinction risk from comparative studies must be interpreted carefully, and in light of the metrics of extinction risk that has been studied. This result is in line with previous studies (Fisher & Owens, 2004; Owens & Bennett, 2000).

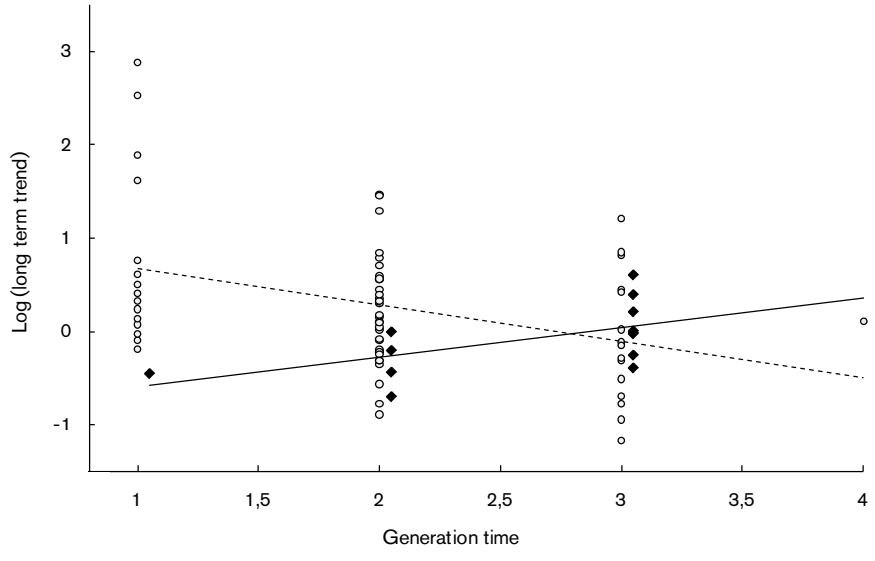

Figure 2. Effect of generation time on the long term population trends (n=77). To visualize the interaction between generation time and overwintering stage, the two overwintering stages adult (♦, solid line) and larvae (○, dashed line) have been separated. The lines represent separately fitted univariate regression lines. To make the graph easier to read the data points for species overwintering as adults have been shifted slightly to the right.

Long-lived species are often more sensitive to increases in mortality, partly because of sensitivity patterns of population growth (Caswell, 2001; Heppell *et al.*, 2000). Negative population trends are often connected to changed mortality patterns (Reynolds, 2003). Our result connecting generation time to population trends therefore indirectly supports this notion.

Theoretical modelling of extinction risk for life history types (III & IV)

Life history types structure the effects of demographic stochasticity (III)

The effects of demographic stochasticity on extinction risk are dependent on the demographic structure of species, but it is unclear how this relates to dimensions of common demographic traits, such as fecundity, survival and maturation age. We found, in general, that extinction risk due to demographic stochasticity increased with fecundity, decreased with maturation age and peaked at intermediate levels of adult survival. Some of these results have been suggested before (Kokko & Ebenhard, 1996; Gilpin, 1992), but we extended the analysis to a wider range of life history types and showed important interaction between demographic traits.

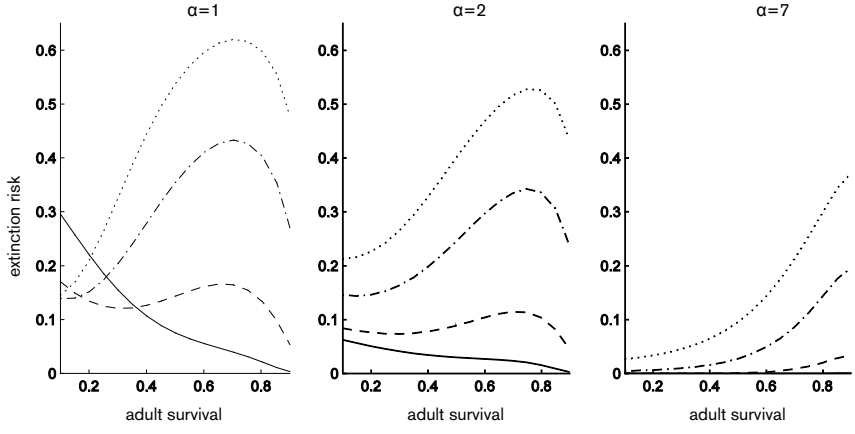

Figure 3. Extinction risk for populations with different adult survival and fecundity, for different values of ago of maturation (left figure α=1, middle figure α=2, right figure α=7). The fecundity of different lines are m=1 (full), m=3 (dashed), m=8 (dot dashed) and m=15(dotted). N0=100, tmax=100, λ=1.

For instance, extinction risk declines with increasing maturation age, but this effect is weaker with high adult survival. We also found that although

extinction risk peaked at intermediate levels of adult survival for life history types with low to intermediate maturation age (Fig. 3), this did not hold at high ages of maturation. For those life history types we instead found increased levels of extinction risk with increasing adult survival (Fig. 3, right panel).

The patterns we found agree well with those found empirically in birds (Saether *et al.*, 2004), except for our observation of increased extinction risk with adult survival at high ages of maturation. We attribute this difference to the fact that Saether et al's data set did not include species with a high age of maturation and low adult survival.

Our results showed that demographic stochasticity cannot be summarily ignored for population sizes over 100 individuals. Furthermore, the results suggest that the rather strong interactions with life history type should be taken into account when evaluating effects of demographic stochasticity on extinction risk. Possible application of this result could be modifications to criteria for evaluating species extinction risk, that are based on life history type, e.g. for setting minimum population sizes, or to define thresholds for when demographic stochasticity can be excluded from population models (i.e. quasi-extinction thresholds). The results are widely applicable, since demographic stochasticity is routinely included in many types of population models (e.g. Population viability analysis), and is indirectly considered in the red list criteria that deals with small population sizes.

On the joint effects of demographic and environmental stochasticity on extinction risk for different life history types (IV)

The effects of demographic stochasticity interacted with life history type (III), but it is unclear if the qualitative patterns between demographic traits and extinction risk remain if environmental variability is taken into account. When only including environmental variation we observed large differences in the stochastic growth rate between life history types. The lowest rates were found in life history types with high fecundity, low age of maturation and low adult survival. Combining the effects of environmental and demographic stochasticity resulted in both additive and interaction effects on extinction risk (Fig. 4). High extinction risks were found in life history types where environmental variation alone caused relatively high extinction risk, but were also found when environmental stochasticity alone caused no or very few extinctions. This effect was most clear at medium and high environmental variances for life history types with an age of maturation of one and two years and intermediate fecundity.

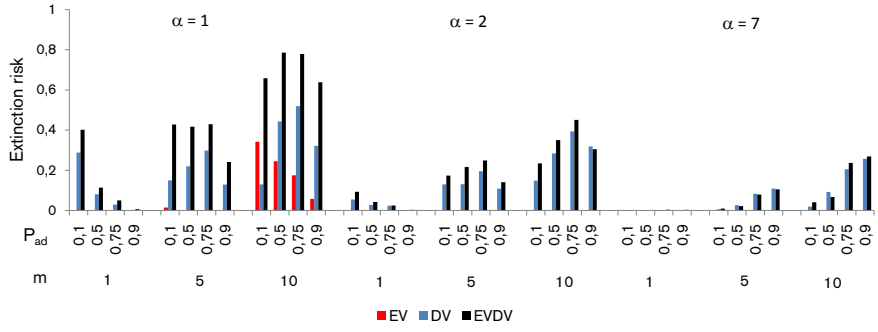

Figure 4. Extinction risk in relation to age of maturation (α), adult survival rate (P_{ad}), and fecundity (m) at intermediate levels of environmental variance (V_e). Differently coloured bars show results from the three different scenarios; only environmental stochasticity (EV), only demographic stochasticity (DV) and both stochasticities (EVDV).

Comparing the qualitative results of this study to paper III showed that many of the patterns found there remained when we included environmental stochasticity, and especially so for life histories with a high age of maturation. However, at medium to high variance and low age of maturation the relationship between adult survival and extinction shifted from peaking at intermediate survivals to being relatively constant over low to intermediate survival, but still decreasing at high adult survival. Short-lived, semelparous species with high fecundity were highly sensitive to the effects of environmental stochasticity. The overall observation from our study that short-lived species were more sensitive environmental variation as compared to long-lived species agree well with Morris et al. (2008).

We view our model as a first step to investigate life history dependent effects of environmental and demographic stochasticity on extinction risk. An important assumption in our model concerns the scaling of environmental variance. We scaled the variance in fecundity by the coefficient of variation, but survivals were compared at absolute levels of variance. Some earlier studies have used a proportional scaling for survival as well (e.g. Jonsson & Ebenman, 2001). We believe that our assumption is reasonable, since a proportional scaling of survival partially goes against the buffered life history hypothesis (Morris & Doak, 2004; Pfister, 1998), which suggests that low variability should be found in demographic parameters that affect growth rates the most. Some empirical evidence also indicates that variance in survival does not generally scale to mean values (Bakker et al., 2009; Arlt et al., 2008; Tirpak et al., 2006; Morris & Doak, 2002; Gould & Nichols, 1998; Kendall, 1998). However, the scaling of environmental variance is largely unknown. Empirical estimates of environmental variance

of demographic parameters need to be compiled and analysed, which could be used to inform environmental variances in theoretical work.

Synthesis

Reflections

The findings from our theoretical studies (III & IV) may appear not to agree with common empirical patterns of species extinction risks. For example, fast life histories (e.g. short-lived birds like the blue tit) are often less threatened by extinction than slow life histories (e.g. long-lived birds like albatrosses), i.e. the empirical pattern of extinction risks is rather the opposite than in our results. There are several obvious explanations for this; 1) small populations are often larger, hence extinction risks are lower, 2) realised population growth rate is usually much higher in small, high fecundity species than in large, low fecundity species thereby reducing extinction risk in the former (Saether & Engen, 2002; Pimm *et al.*, 1988), 3) the reason for higher extinction risk in low fecundity/long-lived species is often that adult survival is reduced because of human impact (Owens & Bennett, 2000); thus a vital rate that has a large impact on population growth, and hence extinction risk, has been changed (Pfister, 1998). In the models presented here, life history types are compared at the same growth rate and small population size, which explain some of the differences between the empirical patterns and our results. Also, paper III only explored the effects of demographic stochasticity, and while paper IV relaxed this assumption we still examined a scenario with comparable levels of environmental variability in all demographic traits. Hence, we are not exploring the effects of deterministic perturbations in means or variances of vital rates due to e.g. habitat modifications or hunting (a subject of retrospective analysis – Caswell, 2001; e.g. Arlt et al, 2008).

We found that long generation times are associated with larger population declines (III), while also being related to low extinction risk due

to demographic stochasticity (through age of maturation - II). These results might seem contradictive, but merely reflects a huge shift in perspective. When paper III dealt explicitly with the dynamics of very small populations, paper II instead studied the associations between species traits and long-term changes in abundance in populations of often wide-spread species. The latter can e.g. be affected by changes in forestry practices or climate, and there is no reason to expect these factors to interact with generation time the same way as the effects of demographic stochasticity.

The result from our comparative study (II) suggested that results from such studies must be interpreted in light of the response variable used to measure extinction risk. This has been observed before (Fisher & Owens, 2004), and implies that generalisation from multiple studies will be difficult, decreasing the possibility for the predictive framework sometimes envisioned (Cardillo *et al.*, 2004; Reynolds, 2003). At the same time, comparative studies have proved that some relationships to predictive variables seem to be fairly robust, cropping up in many individual studies (such as e.g. specialisation, slow life history and body size), which increases the possibility that comparative studies can be used proactively to classify the extinction risk of species.

Possibilities for generalisation

The status of "laws" and generalisation in ecology has been somewhat contended (Lange, 2005; Colyvan & Ginzburg, 2003; Turchin, 2001; Murray, 2000; Lawton, 1999; Cooper, 1998). Some have argued that ecology can and have uncovered strong generalisations/laws, while others suggest that ecology is relegated to studying individual cases, with small prospects of generalised knowledge. I do not comment on this general subject, but since this thesis rests on the possibility of generalised knowledge, I present some reflections on this subject.

We gain knowledge of the world through generalisation and estimation. These two modes of enquiry are complementary, but sometimes with opposing interests, since accurate estimation requires a narrow scope which prohibits easy generalisation. To use generalisations a classification of objects is needed, so that the domain of the generalisation can be delimited (compare to Lawton's (1999) discussion of contingencies in community ecology). A way to understand the problematic status of "laws" and generalisation in ecology is to consider the stability of this classification of objects. In general, scientific disciplines are structured from sciences with an extremely rigid classification, valid over almost infinite time and space (i.e.

physics) to sciences with extremely fragile classifications (i.e. many social sciences) (Winder, 2007). Ecology is somewhere in between these extremes, which is due to evolution, which change study systems over time, the richness and complexity of ecological communities, which change the settings over space and time, and multiple levels of explanation (Dupré, 1993), which can complicate the application of generalisations. This is probably one of the reasons why static laws are so hard to discover in ecology. Realistically, ecological generalisations should be understood in terms of scope in time, space and explanatory level.

The results presented in this thesis obviously differ in their immediate potential for generalisation. Paper III (and IV) presents results that could be very general, but as a consequence leave out many factors known to be of vital importance for understanding the dynamics of some populations. The goals of both these papers are assessments of relative risk. Paper I presents the results of a species assessment (estimated population changes), and these results are clearly taxon specific. However, the methodology is general, and could be directly applied for a wide variety of taxa. Paper II contributes to a body of evidence on extinction risk – species trait relationships, but the direct potential to generalise these results in isolation are limited. However, they can be used as a starting point for understanding extinction risk dynamics in saproxylic beetles.

Practical implications

We find that the use of Natural History Collections can be a feasible way to estimate population trends (I). This means that relative population trends could be estimated for a large number of taxa where there is a general lack of estimates of population change, which would allow wider application of red list criteria dealing with population decline (i.e. criteria A - Gärdenfors, 2005). We also find that, given the spatial scale of our study, population declines are not matched by declines in range, which should caution the use of distributional changes as a substitute of population trends.

The comparative study (II) strengthens the general evidence that specialisation is related to increased levels of extinction risk, in our case in relation to habitat loss. We also found that generation time, adult overwintering stage and adult activity period explained species differences. These results can be used to roughly predict relative extinction risks for species, and could be used to increase the accuracy of the red list (as suggested by Mattila et al., 2008). However, further analysis is needed to determine the generality of our results, and a first test could be to widen the

scope to a larger group of wood living beetles. This is especially relevant since our results revealed that interactions between species traits are important to structure extinction risk in our study. These results could hint at trait interactions found more generally, but might also be taxa specific relationships, due to threatening processes specific to this group of species.

We found that the effect of demographic stochasticity is structured by life history traits (III). This information could be utilised to adjust the population size thresholds used in the classification of population vulnerability due small population size, and base the thresholds on life history characteristics of species. However, it is important to remember that such threshold levels are often derived taking both demographic stochasticity and genetics into account. To test the generality of our findings more empirical studies, such as the one by Saether et al (2004), are needed, preferably spanning a wide variety of life history types and taxa.

When introducing environmental variation to the results from paper III we see that the qualitative patters hold relatively well for species with high age of maturation and longer lived species. In faster life histories the inclusion of environmental variation drastically changed the patterns, which suggests that this factor is essential to assess extinction risk for these. However, the main take-home message from this analysis might be that more empirical studies are needed to establish the relationship between means and variances in survival and fecundity, so that these factors can be appropriately modelled in generic models.

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Svensk sammanfattning

Vi befinner oss i en biodiversitetskris där många arter är hotade av utdöende. Naturvårdsbiologin står inför många olika utmaningar, och den här avhandlingen fokuserar på två huvudspår: (1) uppskattning av populationstrender och (2) ett ramverk som gör det möjligt att identifiera särskilt sårbara populationer baserat på art- och livshistorieegenskaper, vilket skulle kunna leda till en mer proaktiv naturvård. Jag har utnyttjat naturhistoriska samlingar för att uppskatta långsiktiga populationstrender för skalbaggsgruppen långhorningar. Generellt åtföljdes inte negativa populationstrender av minskande utbredning, men utbredningen ökade hos ökande populationer. Detta antyder en uttunning av populationernas täthet, eller möjligen en förlust av delpopulationer på en mindre skala än den som används i vår analys. Analysen visar även hur våra resultat kan användas i rödlistningsprocessen. Jag har även undersökt hur långhorningarnas artegenskaper är relaterade till två olika mått på utdöenderisk (populationstrender och rödlisteklassificering). Detta visade att generationstid, övervintringsstadium, larvens födospecialisering, adult aktivitetsperiod och kroppsstorlek kan förklara utdöenderisker, ofta med samverkan mellan de förklarande variablerna. Dessutom förklarade olika variabler utdöenderisk mätt som populationstrend eller rödlisteklassificering.

Variabilitet i populationsstorlek är en viktig faktor för att avgöra populationers utdöenderisk. Jag har använt populationsmodeller för att undersöka effekterna av demografisk och miljömässig slumpmässighet hos olika livshistorietyper. Med ökande fekunditet och minskande könsmognadsålder ökade utdöenderisken (på grund av demografisk slumpmässighet), medan effekten av adult överlevnad istället samverkade med mognadsålder. När även miljömässig slumpmässighet beaktades visade detta att den kombinerade effekten av båda formerna av slumpmässighet

främst förekom hos kortlivade livshistorietyper (dvs. kortlivade arter med låg könsmognadsålder).

Resultaten visar att information från Naturhistoriska samlingar kan användas för att beräkna långsiktiga populationstrender, och att faktiska populationsminskningar kan underskattas om de baseras på förändringar i artutbredning. Mina studier visar även att livshistorieegenskaper kan användas för att förutse populationers känslighet för utdöende från olika processer, och därmed att vissa typer av arter är mer hotade av utdöende än andra.

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