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The use of historical collections to estimate population trends: A case study using Swedish longhorn beetles (Coleoptera: Cerambycidae)

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Abstract

Long term data to estimate population trends among species are generally lacking. However, Natural History Collections (NHCs) can provide such information, but may suffer from biases due to varying sampling effort. To analyze population trends and range-abundance dynamics of Swedish longhorn beetles (Coleoptera: Cerambycidae), we used collections of 108 species stretching over 100 years. We controlled for varying sampling effort by using the total number of database records as a reference for non-red-listed species. Because the general frequency of red-listed species increased over time, a separate estimate of sampling effort was used for that group. We observed large interspecific variation in population changes, from declines of 60% to several hundred percent increases. Most species showed stable or increasing ranges, whereas few seemed to decline in range. Among increasing species, rare species seemed to expand their range more than common species did, but this pattern was not observed in declining species. Historically, rare species did not seem to be at larger risk of local extinction, and population declines were mostly due to lower population density and not loss of sub-populations. We also evaluated the species' declines under IUCN red-list criterion A, and four currently not red-listed species meet the suggested threshold for Near Threatened (NT). The results also suggested that species' declines may be overlooked if estimated only from changes in species range.

Keywords: Population trends, Natural history collection (NHC), Range-abundance dynamics, IUCN Red list, Species conservation, Population dynamics, museum data, Coleoptera: Cerambycidae.

1 Introduction

The current loss of biodiversity is rapid with unprecedented rates of species' declines and extinctions [33, 47]. Local extirpations and population declines can both have detrimental effects on ecosystems function and services (i.e. [4, 36]). Although it is well documented that populations of species decline or go extinct [23, 59], we lack quantitative information on rates of population decline for the majority of species. Assessing the rate of population change often requires a proxy for population size, which is usually acquired from standardised population counts from long-term inventories. Unfortunately, for most species such long-term time series are not available, thus an alternative is to use other proxies of population size such as natural history collections (NHC) or hunting/fishing bag rates [53, 60]. A benefit of using such alternative proxies is that they allow us to use historical data, whereas this is seldom available for

direct population counts. This aspect is clearly valuable, since an excessive focus on recent abundance patterns can be misleading when analysing causes of population change, and the time window may be too short to reveal natural patterns of population size fluctuations [52]. A major drawback in using historical collections, however, is that such data sources in most cases are based on non-standardised sampling methods. Thus one needs to consider potential biases in the data, such as changes in sampling effort, changes in sampling methods and the effects of increased knowledge on species biology.

1.1 Using NHC data for estimating trends

NHCs are records of biological material collected by expeditions, professional biologists and amateurs. They encompass all major taxonomic groups, but at different frequencies and time frames (from tens to hundreds of years). The ecological value of NHCs was recognised in the mid 1990s [8, 32, 41, 52], but also see [14], and since then studies utilizing information from

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NHCs fall into three general categories: they aim to (1) estimate the probability that a species is or will go extinct [43], (2) study temporal trends in species abundance or range [13, 27], or (3) estimate community features such as species richness [24, 42, 46].

When estimating population trends, species data from NHCs have several characteristics that are potential sources of bias: (1) *No records of absences* – There is usually no knowledge about species absences, making it difficult to know whether a lack of records is due to species absence, non-detection (e.g. from stratified presence/absence studies) or that the location has not been visited (e.g. for presence only data); the real reason is, however, usually unknown [37]; (2) *Changes in sampling effort* – It cannot be assumed that the sampling effort has been constant over time, because NHCs usually stem from many years and many sources. Therefore, the yearly number of records of a specific species is not only dependent on the population size, but also on the yearly sampling effort; (3) *Changes in spatial coverage of sampling* – Three possible biases may arise. First, if the sampled area is constant, population increases due to expansion of the distribution may remain undetected. Second, if the sampled area changes with time, perceived population changes may not be real [21, 57]. Third, different collectors may recognize a name of a location as different in extension, giving the impression of changed spatial coverage; (4) *Changes of collection methods* – New knowledge on species' biology and new collection methods may increase species detection and collection, resulting in apparent but not necessarily true positive population trends; (5) *The attractiveness to collect a certain species may change* – NHCs depend on the willingness of collectors to collect specimens of different species. The attractiveness of a species is, among other things, influenced by the charisma of its visual characteristics, its sensitivity to human-induced habitat changes, its rarity, its red-list status, or its protection status. If any of these factors change with time, so may the collection effort for the species.

1.2 Causes of population changes

While population changes are regulated by many factors, declines are often linked to a reduction or degradation of existing habitat. When available habitat is reduced, associated population declines will be accompanied by a proportional reduction in the range of the focal species, whereas habitat degradation may result in population decline via a reduction in species density which is unrelated to a change in range [20]. These two avenues to population decline are not mutually exclusive, and may occur simultaneously or in temporal sequence, e.g. changes in habitat quality may reduce population density in sub-populations, which then increases the risk of local extinction because of demographic stochasticity and loss of genetic variation [25]. This leads to the prediction that range contractions are more likely to be linked to popula-

tion declines in rare species but not necessarily in common species. Population declines and increased extinction risk are often positively correlated with the degree of habitat or resource specialization of the species, since species that are more specialized are assumed to be more sensitive to environmental changes [18]. Thus, specialized species would be expected to be overrepresented among species experiencing population decline. This expectation will, however, rest on the assumption that the required habitat or resource of the specialized species is diminishing or deteriorating, and that population declines are mainly caused by habitat degradation.

Turning to increasing species, analogous patterns of density and range dynamics may occur. Population densities may increase without range expansion or there may be range expansions due to colonization of new areas but no increase in density, or population density and range both increase [19]. In contrast to declining species, however, it is difficult to make any general predictions on how these dynamics may relate to the commonness of a species. One key factor is colonization ability which is a complex and difficult variable to estimate, as it depends on dispersal ability, demographic traits and degree of specialization [19]. However, common species may have already filled areas of suitable habitat; thus range cannot expand in contrast to less-common species which may still have the opportunity to invade vacant suitable habitats [19, 28, 62]. This suggests that from a habitat filling aspect it can be predicted that as populations increase, less-common species should expand their range more than common species [19]. Thus, knowing the relationship between changes in population size and range can have important implications for species conservation. The question is whether observed changes of species' distributions can be used as indicators of population changes, especially when there are non-linear relationships between the two variables [20]. Increasing population densities have also been observed due to temporary crowding effects following habitat destruction or fragmentation [5, 12, 58], but that is usually found on relatively small spatial scales. These transient effects are also rapid in short lived species such as insects [18, 45], which makes them less relevant for long term studies.

In this study we analyse a comprehensive data set consisting of records of Swedish longhorn beetles (Cerambycidae, Coleoptera), with the aim of estimating population trends over the last 100 years, and to investigate whether changes in population abundances are related to changes in population range. In the analysis, we use the total number of yearly records of all species as an estimate of effort to calculate relative species abundances, and account for the number of active collectors. To understand the dynamics behind the range-abundance relationships, we test whether changes in population size are accompanied by changes in range, and if this interacts with rarity. We also test whether the degree of substrate specialization explains how species' abundances change tem-

porally. Finally, we use the results to evaluate species under IUCN red-list criterion for population decline, and discuss implications for species' conservation.

2 Methods

2.1 Data and variables

In Sweden, 117 species of longhorn beetles have been found occurring naturally in Sweden during the 19th–20th century [16]. Fifty species (approx. 45% of the Swedish species) are currently listed on the Swedish Red List [23], out of which 22 are categorized as threatened (VU, EN or CR; see appendix for description) and 5 as Regionally Extinct (RE). Nomenclature in this study was based on Ehnström and Holmer [16]. Longhorn beetles are, in comparison to many other groups of insects, well known and relatively easy to identify, and this has resulted in a large number of NHC records. Most species are saproxylic and their larvae depend on dying or dead-wood substrates, but a few species feed on alternative substrates such as living trees, herb roots or litter. In general, an estimated 20–25% of all forest living insects in Sweden depend on dead-wood substrates [54], so knowledge of population trends over the last century in one taxon using these substrates may be indicative of many other species utilizing the same substrates. Larval development times generally lie between one and five years [16], but can be much longer for some species. The adults are believed to be relatively short lived, although comprehensive information on longevity is almost lacking. No species produces more than one generation within the same year. Changes in human land use in forests during the last two centuries [3, 34, 56, 54] and the agricultural landscape [29], have affected the amount and quality of wood substrates, and the changes have accelerated over the 20th century due to intensified forestry. Many longhorn beetle species are considered to be declining as a consequence of these changes, with the largest perceived threats being human-induced habitat destruction or degradation [16], as well as small or few sub-populations [23].

A database of species records was compiled during 2000–2008. Here, a record refers to an individual account of a collected beetle, stemming either from a physical specimen or a literature account, that includes information on the location and date of the collection event. Since few records included information on whether one or several individuals were found, we excluded this information in the analysis. If several records existed from the same collection event, e.g. from different museum collections, duplicates were removed. The sources used were museums, private collections, records from the Swedish Species Information centre, fauna literature, entomological periodicals, and written reports from the Swedish Environmental Protection Agency and county boards. Records were also obtained from some local author-

ities, inventories of key habitats, and other reports and publications. The museum sources include the major natural history museums, university collections, provincial museums, and former college collections. Collectors were first contacted collectively through an advertisement in the entomological periodical 'Entomologisk tidskrift' in 2001. As this request generated little response, about two hundred members of the Swedish Entomological Society with a stated interest in beetles, wood-living insects, forest insects or conservation were contacted individually. In the end, 138 individual collectors made their records or collections available. For a full description of the database, see Lindhe et al. [35]. The database spans records from the 18th century to present time, but only records from the 20th century have the quality and resolution necessary for assessing changes of species' abundance. All entries were assigned georeferenced coordinates according to the Swedish geographical referencing system 'Rikets nät' (RT90).

The NHC data is the result of collections made by expeditions, amateur entomologists and researchers and is therefore normally not standardised or randomly selected. The appearance of a record of occurrence in the database is the endpoint in the chain of events where a collector: (1) visits an area where the species is present, (2) encounters the species, (3) collects a specimen, and (4) identifies and mounts the specimen, (5) preserves it in a collection, (6) the record is made available for us to study. Thus, a common species may be encountered (2), but not collected (3), whereas a rare species, once encountered, is more likely to pass through all the steps. The number of visits to localities where a species is present (1) may vary over time, affecting the number of collections of this species. This factor is likely to be correlated to the number of active collectors, since more collectors probably mean a larger spatial coverage of the search effort. For some records, such as records based on the literature, some steps in the chain can be bypassed (No. 5) or slightly modified (No. 6 representing publication). To minimize bias in species trends, biases over time and space that affect the links in the chain of events described above need to be identified and accounted for as far as possible.

To minimize the effect of changes in collection methods and collector's behaviour we excluded records of specimens labelled as collected in traps, records based on larvae feeding galleries, and records referring to specimens hatched from larvae in collected substrate. Therefore, only records that can be assumed to stem from collectors actively searching for the species in the field have been used in the analyses. Furthermore, all records made before year 1901 or after year 2000 were excluded, the old records due to their low information content, the very recent because we expect a lag between the collecting of specimens and their appearance in a collection or a museum, and because the database has not been continuously updated since the first compilation. Thus, all analyses are based on 20th century, actively searched

for and handpicked specimens. In the final analysis the subset of the database that we used consisted of 42,931 records from 108 species. For the generalized mixed model (see Section 2.2) we also removed records not tied to a specific location.

The first Swedish Red List that included longhorn beetles was published in 1986 [1, 17], and since then a varying number of longhorn beetles has been included in different versions of the Red List. Our expectation was that the inclusion on a Red List led to an increased effort to survey these species especially in the 80s and 90s. To take into account that red-listed and non red-listed species have been sampled differently we classified all species in our database as those that have been red-listed at least once over time (in the following denoted as red-listed, in total 59 species) and those that have not. We included all the Swedish Red Lists or similar classifications of threatened species, both the newer ones applying the IUCN (IUCN 2001) quantitative criteria [22, 23] and the older qualitative systems [1, 15, 17].

To adjust for the change of overall collection effort over time, we used the yearly sampling intensity as reflected by records in the database as an estimate of sampling effort. Thus, for each species a yearly Population Size Index (PSI) was calculated as:

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

As an estimate of species' specific *Sampling effort*, we used the total number of yearly records of all non-red-listed species from the Swedish provinces ('Landskap') where the focal species was found during the study period. Thus, rather than just an estimate of collecting activities at the national level, the relevant sampling effort is restricted to areas where the species has been found. Only non-red-listed species were used for the estimation of sampling effort, since the sampling intensity of red-listed species has changed over time (see below). Our method yields a yearly frequency of each species, relative to the overall sampling effort, and this quantity is used as a proxy for species abundance. The approach is similar to Hedenäs et al.[27] and Ponder et al.'s [48] use of background groups. As records of the same species from the same local area and period of time may be seen as interdependent to a certain extent, we combined merged any records from the same locality (the second lowest site classification used in the database – used with town or general area), month and year before calculating the indices.

Since the sampling of longhorn beetles before 1918 was of a lower intensity than later years and therefore probably more uncertain (Fig. 1a), all analyses only used data from 1918 and forward. Preliminary analyses showed a general increase in number of records of red-listed species over time (Fig.1d). This pattern probably reflects an increasing focus on rare species rather than real increases in abundance. The increased interest in red-listed species can be seen

as a gradual shift in the attitudes and priorities of collectors, demonstrated in the functional relationship between number of records of red-listed species and time. Therefore, we used the average trend in the yearly frequency of red-listed species (Fig.1d) as the background against which red-listed species were compared. To characterize the average trend of red-listed species we fitted several generic functions that could be expected to capture the overall pattern (Sigmoid, Gompertz, Holling disc, linear polynomial, quadratic polynomial). As model selection criteria, we used AICc [9]. The Gompertz function was used for later analysis, since it provided the best fit to the data (AICc= -63.5; next best model AICc= -62.3), with parameters $\alpha = 0.134$, $\beta=0.064$, $\gamma=48.3$:

$$y(t) = \alpha e^{-e^{-\beta(t-\gamma)}}$$

For red-listed species, the predicted yearly values from the selected function were used to adjust our estimate of effort. Consequently, the PSI of red-listed species was calculated in relation to the average trend of all red-listed species, not in relation to other species. Since a number of red-listed species were not found in Sweden until late in the 20th century, the average trend for red-listed species was modelled only on species that occurred in the database before 1930.

An observed change in species' range can be due to an actual change in species range, a change in spatial sampling effort or both. We wanted to determine if a change in PSI was related to a change in range, therefore the direct measure of species' range, as grid cell occurrences, did not suffice as it can be influenced by spatial sampling effort. To separate changes in range and sampling we calculated a yearly relative species' range, using a centred moving window. The total occupancy of grid cells using all records in the window, i.e. including all species, was calculated as a measure of spatial sampling effort. As above, only records from provinces where the focal species has been found was used. The relative species range was then estimated as the number of grid cells occupied by the focal species divided by the total number of occupied grid cells with records of longhorn beetles, i.e. the spatial sampling effort. A similar solution was put forward by Ponder et al.[48] in their use of background data as pseudo-absences, and evaluated by Joseph and Possingham[31]. We used a moving window centred on the year of focus to smooth the distributional changes over time. The moving window was 11 years wide and the grid size used to calculate occupancy was $100 \times 100\text{km}^2$. To quantify the overall change in relative species range between time periods we calculated the proportional change by pooling all records from each time period (for time periods see Section 2.2). Proportional changes of grid occurrences at a relatively large scale has been shown to work well as a proxy for detecting changes in range at smaller scales, and does not require scale correction [31]. As a higher number of collectors can result in a larger spatial coverage of species sampling –

more collectors may cover wider areas on a local level and/or visit a wider range of habitats – we calculated the yearly number of collectors represented in the database from the area where the species was found, and used this as a covariate in the analysis. Both proportional changes of grid occurrences and number of collectors were standardised to zero mean and unit variance before the analysis. The total number of records of each species in the database, after the modifications described above, was used as a proxy for the species' overall rarity. The degree of species specialization was determined as the number of larval host plant species used in Sweden [16].

2.2 Statistical analysis

A comparison of species frequency between time periods was performed using a generalized linear model. We compared three 20 year time periods, coded as a class variable, namely 1921–1940 (p1), 1951–1970 (p2) and 1981–2000 (p3). We chose these specific periods to obtain estimates of long and shorter term changes between evenly spaced points in time. The natural logarithm of sampling effort was used as model offset. The data show overdispersion, so we used the negative binomial function as distribution function, with a log link. The analysis was performed using Proc GENMOD [50]. The relationship between estimated changes in the PSI or relative species range and species traits were analysed with general linear models using Proc GLM [50]. To test if the effect on range differs between rare and common species and increasing or decreasing species, we fitted a model with increasing/decreasing as a class variable, and tested the interaction effect between this class variable and rarity (measured as the logarithm of number of records). This analysis is focused on the recent changes in range and abundance, i.e. between p2 and p3.

In additions to the overall changes in the PSI and range between time periods, and how these relate to each other, we explored the continuous effects of the predictive variables on the PSI. To that end, we performed a generalized linear mixed model analysis. The model included a 2nd degree polynomial of time, relative species range, and the number of collectors. The aim was to partition the change in the PSI between contributions from range and the overall time trend, while controlling for number of collectors. Since we used an 11-year moving window to estimate range, the years used in the analysis were 1923–1995. As in the previous model, we used the negative binomial function as distribution function, and the natural logarithm of sampling effort was used as model offset. The full model included:

$$\begin{aligned} \text{Population size index} &\sim \text{time}, \text{time}^2, \\ &\text{relative species range}, \text{collectors} \end{aligned}$$

Because population sizes of adjacent years can be cor-

related, we modelled the correlation between years using a negative exponential relationship. We also evaluated other correlation structures, such as a power relationship, but this did not change the results in any significant way. The analysis was performed using Proc GLIMMIX [51]. The full model was reduced using backward elimination. We removed the factor with the largest p -value first, but removed $time^2$ before $time$ if both factors were non-significant. We did not remove $time$ if $time^2$ was significant, since these terms together merely serve to produce a description of temporal trend [55]. The elimination stopped when all factors had a p -value smaller than 0.1. To improve the variable estimates in the final model we removed outliers with a studentized residual larger than 3. The reason that we did not remove outliers earlier in the modelling process was to follow a conservative approach, and this did usually not affect the structure of the final model, only the variable estimates from the final model. We did not use information criteria, such as AICc, for model selection, because the pseudo-likelihoods that are used for model estimation in the GLIMMIX procedure cannot be used for model comparisons [51]. Because of problems with model convergence for species with few records and considerations of sample size, the analysis was performed only for species with more than 100 records in the 20th century. An effect of this selection criteria was that only 14 out of the 50 currently red-listed longhorn species [23] were analysed. We compared the frequency of predictor variables being significant between red-listed and non-red-listed species using chi square tests.

Collinearity between predictor variables can influence the model reduction process, and a model of significant factors does not necessarily equate to the model with most explanatory power [38]. To complement the significance tests from the model reduction exercise, and to evaluate how much of the explained variation that can be independently attributed to each predictive variable, we performed a hierarchical partitioning analysis [10, 38]. Hierarchical partitioning evaluates all 2^k sub-models, based on the k predictor variables, and calculates the independent proportional influence of each variable based on all model combinations where the variable is present. The comparison between sub-models is based on a goodness of fit criterion. In our analysis, we used the model deviance to estimate goodness of fit and modelled the response variable as a Poisson distribution with the natural logarithm of collection effort used as model offset. The analysis was performed in R [49] with a modified version of the hier.part package [61], to accommodate for using a model offset and the deviance as goodness of fit criterion. The independent effects (I%) for each variable show how much of the total variation that is independently explained by this factor, and the change in deviance (Δ Deviance) show the percentage difference in deviance between the intercept model and the full model.

Table 1: Generalized linear model of *Population Size Index* (PSI) with time as class variable for longhorn beetles with more than 100 records in the 20th century in Sweden. The time periods used are 1921–1940=‘1’, 1951–1970=‘2’, 1981–2000=‘3’. The model uses the negative binomial as distribution function. Yearly sampling effort (as described in methods) is used as offset. Estimates show changes in PSI between time periods, where 0 is no change and 1 reflect a 100 percent change. Positive numbers indicate an increase with time whereas negative numbers is a decrease. *P*-values: * *p* < 0.05; ** *p* < 0.01; *** *p* < 0.001; no asterisk means not significant (*p* > 0.05). Species that are placed on the current Swedish Red List [23] are identified by their current red list category after the species name, and species that were listed on earlier red lists, but are now removed, are denoted by (rl).

Species	Model					Species	Model				
	p-value	3 vs 1	3 vs 2	2 vs 1	p-value		3 vs 1	3 vs 2	2 vs 1		
<i>Acanthocinus aedilis</i>	**	-0,36***	-0,25*	-0,14	***	<i>Obera oculata</i>	-0,08	-0,16	0,09		
<i>Acanopops septentrionis</i> (NT)	***	-0,4	1,28**	-0,74***	***	<i>Oplostia cinerea</i> (rl)	2,64*	-0,44**	5,45**		
<i>Agomorphus clavipes</i> (rl)	*	0,35	0,62**	-0,17	**	<i>Oxymirus cursor</i>	0,02	0,11	-0,09		
<i>Agapanthia villosivirescens</i>	***	11,55***	2,61***	2,48	**	<i>Pachyta lamed</i>	-0,5***	-0,27	-0,32*		
<i>Alosterna tabacicolor</i>	***	0,42***	0,37***	0,03		<i>Pedostrangalia pubescens</i> (rl)	0,19	0,4	-0,15		
<i>Anaglyptus mysticus</i> (NT)		0,01	0,12	-0,1	***	<i>Phymatodes alni</i> (NT)	0,5	-0,07	0,61		
<i>Anastrangalia reji</i>	**	-0,19	0,74***	-0,53***	***	<i>Phymatodes testaceus</i>	1,03***	0,32*	0,54*		
<i>Anoplodera sanguinolenta</i>	***	-0,27**	0,01	-0,27***	**	<i>Phytoecia cylindrica</i>	0,39	0,28	0,09		
<i>Anoplodera saxguthata</i> (NT)	***	3,36***	1,65***	0,65	**	<i>Platyonotus arcuatus</i>	0,81***	0,4*	0,29		
<i>Arhopalus rusticus</i>		0,02	-0,09	0,13	**	<i>Pogonocherus decoratus</i>	0,84*	0,07	0,72		
<i>Aromia moschata</i>		-0,11	0,25	-0,28*	**	<i>Pogonocherus fasciculatus</i>	-0,32**	-0,32**	0,01		
<i>Asemum striatum</i>		-0,18	-0,05	-0,14	**	<i>Pogonocherus hispidulus</i> (rl)	0,24	1,11*	-0,41		
<i>Brachyta interrogatioris</i>		-0,17	-0,09	-0,09	**	<i>Pogonocherus hispidus</i>	-0,02	-0,33**	0,45*		
<i>Callidium coriaceum</i> (rl)		0,17	0,86*	-0,37	***	<i>Prionus coriarius</i> (NT)	-0,61***	-0,35*	-0,4**		
<i>Callidium violaceum</i>	***	-0,59***	-0,46***	-0,24**	***	<i>Pyrrhidium sanguineum</i> (NT)	4,02**	1,22**	1,26		
<i>Cerambyx scopolii</i> (NT)		-0,22	0,03	-0,24		<i>Rhagium inquisitor</i>	0	-0,15	0,18		
<i>Chlorophorus herbstii</i> (VU)	**	-0,54	-0,76***	0,89	***	<i>Rhagium mordax</i>	-0,18*	0,03	-0,2*		
<i>Clytus arcticus</i>	***	0,74***	0,33***	0,31*		<i>Rhagium sycophanta</i> (VU)	-0,5***	-0,41***	-0,15		
<i>Cortodera femorata</i>	**	3,3**	0,95*	1,21		<i>Rutpela maculata</i>	0,11	0,03	0,07		
<i>Dinoptera collaris</i>	**	0,57**	0,08	0,45*		<i>Saperda carcharias</i>	0,05	-0,08	0,14		
<i>Engates faber</i>		0,12	-0,34	0,71		<i>Saperda perforata</i> (rl)	0,74	0,05	0,65		
<i>Exocentrus lusitanus</i>	**	0,39	-0,61**	2,54**		<i>Saperda populnea</i>	-0,2	-0,09	-0,13		
<i>Gaurotes virginea</i>	**	-0,14	-0,18	0,05		<i>Saperda scalaris</i>	-0,09	0,15	-0,21*		
<i>Gnathacmopsis pratensis</i>	**	-0,54***	-0,19	-0,43**		<i>Semanotus undatus</i>	-0,35*	-0,12	-0,26		
<i>Grammoptera ruficornis</i>	**	0,65***	0,13	0,46**		<i>Spondylis buprestoides</i>	-0,22*	-0,22*	0		
<i>Grammoptera ustulata</i> (NT)	***	5,62***	0,43	3,64*	*	<i>Stenocorus meridianus</i>	0,1	0,11	-0,01		
<i>Hylotrupes bajulus</i>	***	-0,69***	-0,54***	-0,34*	**	<i>Stenostola dubia</i>	0,76*	-0,01	0,78*		
<i>Judolia seamaculata</i>		-0,09	0,07	-0,15	**	<i>Stenurella melanura</i>	-0,27**	-0,12	-0,17		
<i>Lamia textor</i>	***	0,56*	0,11	0,41	***	<i>Stenurella nigra</i>	1,21***	0,21	0,84**		
<i>Leipus nebulosus</i>	***	0,85**	-0,19	1,27***	***	<i>Stictoleptura maculicornis</i>	-0,43***	-0,31***	-0,17*		
<i>Leptura quadrifasciata</i>	***	-0,25***	0,07	-0,29***	***	<i>Stictoleptura rubra</i>	-0,3***	-0,19***	-0,14		
<i>Lepturobosca virens</i>	*	-0,27	0,25	-0,41**	***	<i>Stictoleptura scutellata</i> (VU)	2,36**	2,35***	0		
<i>Mesosa nebulosa</i> (NT)	**	-0,01	-0,5*	1	***	<i>Strangalia attenuata</i> (VU)	0,48	0,6	-0,08		
<i>Molorchus minor</i>	**	0,49**	0,33*	0,12	***	<i>Tetropium castaneum</i>	-0,03	-0,13	0,12		
<i>Molorchus umbellatarum</i>		1,26*	0,41	0,6	***	<i>Tetropium fuscum</i>	1,14***	0,13	0,88**		
<i>Monochamus galloprovincialis</i> (rl)		0,27	0,21	0,04	**	<i>Tetrops praeusta</i>	0,15	-0,32*	0,68**		
<i>Monochamus sutor</i>		0,08	0,14	-0,05	***	<i>Tragosoma deparsium</i> (VU)	0,52	0,46	0,04		
<i>Necydalis major</i> (rl)	*	1,34**	0,11	1,11*	***	<i>Xylotrechus rusticus</i>	1,33***	1,08***	0,12		
<i>Nothorhina muricata</i> (NT)	***	16,84**	0,79*	8,95*							

3 Results

3.1 Records and sampling effort over time

The overall number of records, and hence the general sampling effort, increased during the 20th century (Fig. 1a). The inflection point of the Gompertz function was estimated to 1948, which indicates that the increased collection of red-listed species started well before the Red List was introduced. At about the same time, the number of records, the number of collectors and the total number of species appear to have roughly reached asymptotic levels (Fig. 1a–c). The number of species of non red-listed species, however, had already approached the asymptotic level around 1920 (Fig 1b).

3.2 Temporal trends in population size

When using time period as a class variable 55% (42) of the species showed significant differences in *Population Size Index* (PSI) between time periods, and 46% (35 species) showed significant differences between the first (p1: 1921–1940) and the last (p3: 1981–2000) time periods (Table 1). Out of the 35 species, 40% showed a decrease and 60% an increase in the *Population Size Index*. The proportion of significant change from the first to the last time period among red-listed species was approximately the same, 42%. The estimated changes are also quite large, with many species showing 25–60% declines between the first and the last periods, while indices of others, often quite rare species, showed dramatic increases. Later changes (from p2: 1951–1970) were of a similar magnitude. Figure 2 shows the histograms of changes in PSI for time periods p2–p3 and p1–p3. The distributions are approximately normal for both contrasts, but with an excess of large positive changes between p1 and p3.

3.3 Range-abundance relationships

There was a weak overall positive relationship between the change in relative species range and change in PSI between p2 and p3 ($r^2 = 0.19$, $p < 0.001$). Change in relative species range for increasing species was negatively related to number of records (ANCOVA post-hoc test; $t = 6.18$, $p < 0.001$) whereas there was no such significant relationship for decreasing species ($t = 0.97$, $p = 0.34$, Fig. 3); this interaction was significant (interaction $\log(\text{number of records}) \times \text{category}$: $F = 7.43$, $p < 0.01$; the model was $\Delta \text{range} \sim \text{category}$, $\log(\text{number of records})$, $\log(\text{number of records}) \times \text{category}$, i.e. a separate intercepts model). The results were qualitatively unchanged when the change in PSI (Table 2.2) was inserted as a predictor with separate slopes between classes, or if the change in range was calculated on raw grid numbers instead of relative species range.

3.4 Factors explaining temporal changes in PSI

Time and range were the two variables that most often explained the variation in the PSI (Supplementary information). Across all species there was, however, a large statistical range as to what extent the predictors explained variation in PSI (range of $\Delta \text{Deviance} = 0\text{--}55\%$, Supplementary information)

For most species, a linear effect of time and relative range seemed to predict variation in PSI better than the number of collectors (Fig. 4). The same pattern was present for both methods of analysis, i.e. GLMM significance tests and independent effect from hierarchical partitioning. The frequency of significant explanatory variables did not differ between red-listed and non-red-listed species for any variables (χ^2 -values: $\text{time} = 0.07$, $\text{time}^2 = 0.49$, $\text{range} = 0.00$, $\text{collectors} = 0.27$, $p > 0.1$ for all tests – low sample sizes in some classes). The two methods generally identified the same predictor variables as the most important ones, the species-wise concordance between GLMM significance and hierarchical partitioning was 81%. When calculating the concordance we pooled the two time factors, so the three categories were *time*, *relative species range* and *collectors*.

To assess if range is a more powerful predictor of PSI for rare species than common ones, we plotted the model estimates of the range variable for species where it was significant against species frequency in the database (Fig. 5). This plot revealed that range had a larger effect on PSI for rarer species. ($n = 36$, $t = 3.54$, $p < 0.01$, $r^2 = 0.27$). The regression of change in PSI on the number of larval host species was not significant for either of the time periods, with the effect close to zero ($p > 0.2$ for both time periods).

3.5 Threatened species

The PSI could be used to classify species according to IUCN red-list criterion A2 (IUCN 2001). When using the most recent change, period 2–3, only one species, *Chlorophorus herbstii*, showed an interpolated population decline that meets the threshold for Vulnerable (VU) A2 (=30 % decline over 10 years). According to the guidelines for applying the IUCN Criteria for the Swedish Red List evaluation, a 15 % decline over 10 years (or three generations) can be used as a lower threshold for classifying species as Near Threatened (NT) according to criterion A [23]. Additional species that declined in PSI to meet this threshold included *Callidium violaceum*, *Exocentrus lusitanus*, *Hylotrupes bajulus*, *Mesosa nebulosa*, *Oplosia cinerea*, and *Rhagium sycophanta*. Four of these species are not currently red listed, and the other three are red listed based on other criteria than population trends. If the results from this study are viewed as underestimations of the real trend, a smaller significant change such as 5 % decline over 10 years may be deemed noteworthy. Additional species that meet that level

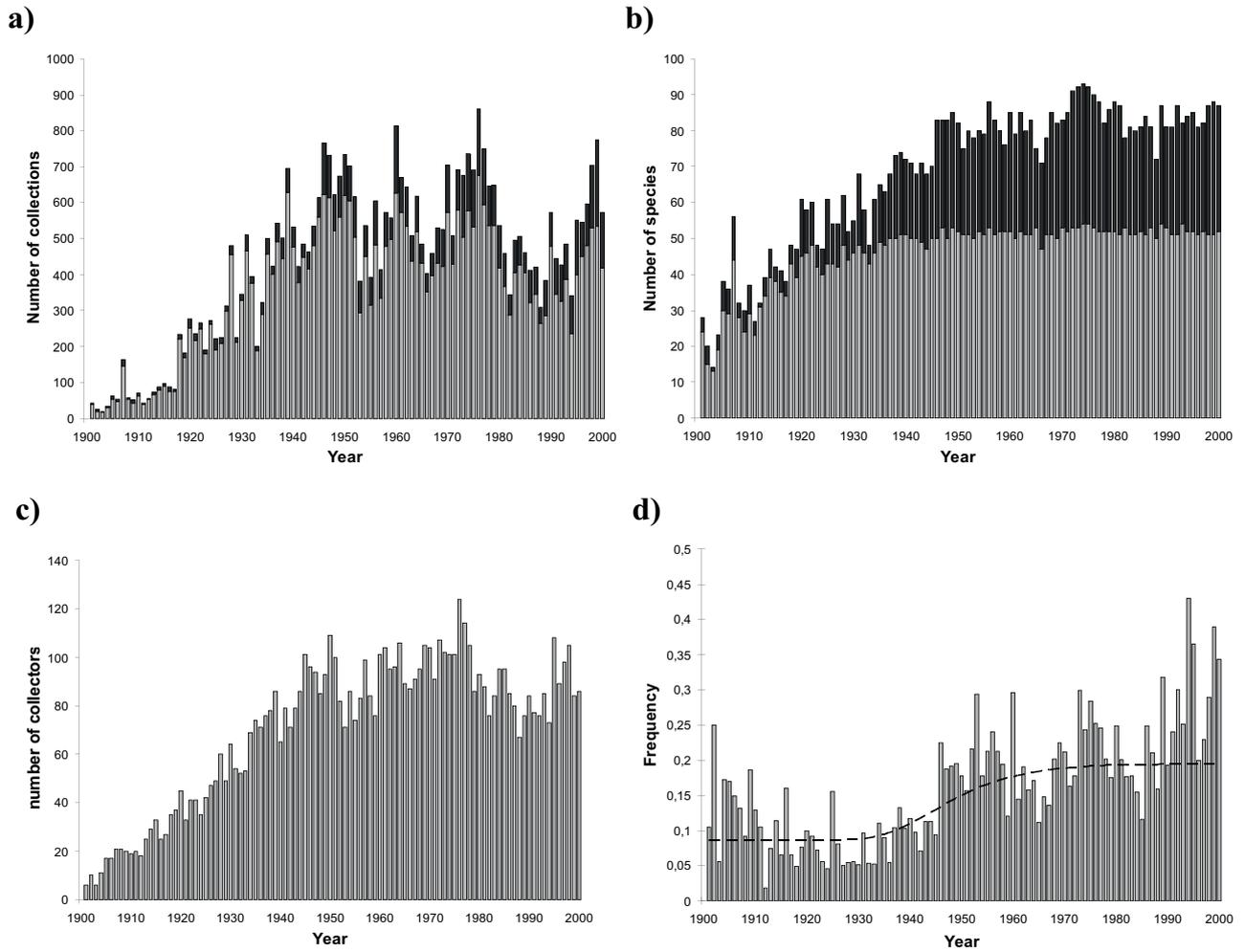


Figure 1: Descriptive statistics of the database. a) Total number of records per year. b) Total number of species per year. c) Total number of collectors per year. d) Relative frequency of red-listed species out of total records. The hatched line corresponds to the fitted Gompertz function, used to adjust the sampling effort for red listed species. For figure 1a and 1b, the light grey bars represent non red-listed species and the dark grey bars represent red-listed species.

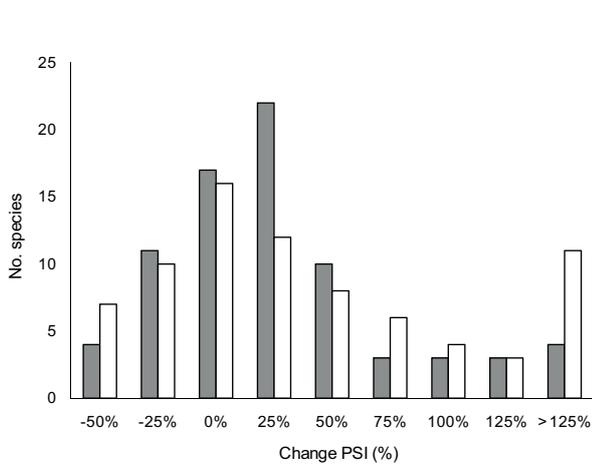


Figure 2: Histogram of changes in *Population size index* between time periods p2 and p3 (grey bars) and p1 and p3 (open bars).

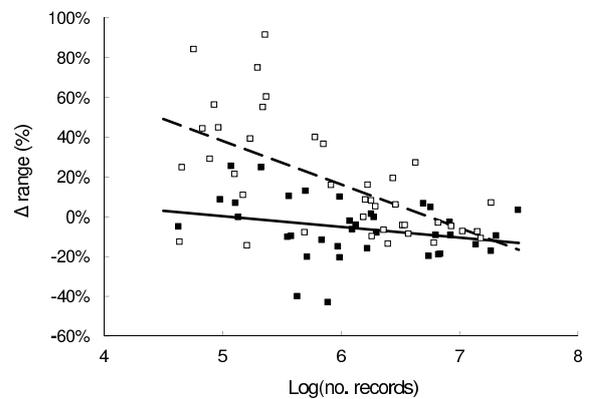


Figure 3: The relationship between the change in relative species range and log(number of records) for increasing and decreasing species. Open squares and dashed line is for increasing species, and closed squares and solid line is for decreasing species. Higher values of log(no. records) represents more common species.

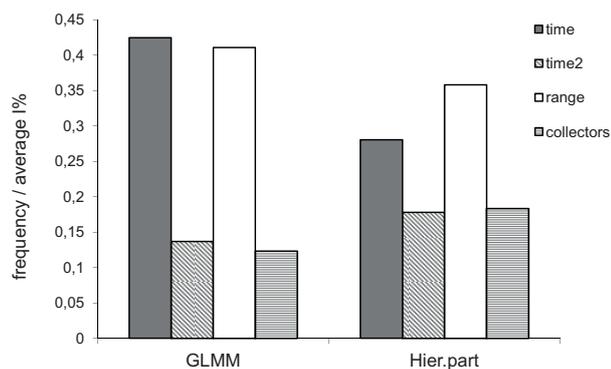


Figure 4: The frequency of each explanatory variable being significant in the generalized mixed linear model, $n = 73$ (left series), and the average individual effect in percent from hierarchical partitioning (right series). Note that the left series does not sum to 1, since each species does not necessarily have only one significant explanatory variable.

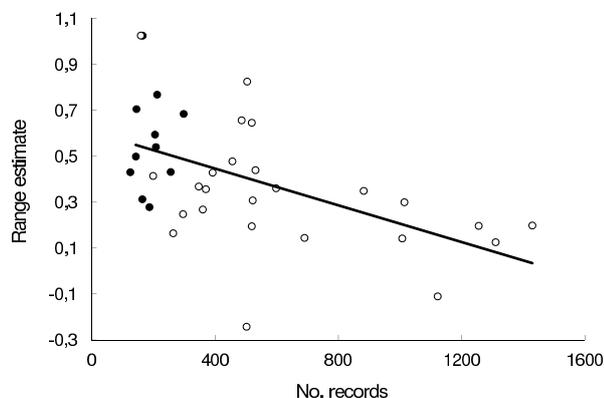


Figure 5: Estimates of the range variable coefficient against the species frequency in the database ($n = 36$, $t = 3.54$, $p < 0.01$, $r^2 = 0.27$). Open symbols correspond to non red-listed species and closed symbols to species that are or have been red listed.

of decline were *Acanthocinus aedilis*, *Stictoleptura maculicornis*, *Stictoleptura rubra*, *Pogonocherus fasciculatus*, *Pogonocherus hispidus*, *Prionus coriarius* and *Tetrops praeusta*.

4 Discussion

More than half of the Swedish longhorn species appeared to have changed in population size during the study time, as indicated by significant differences in the Population Size Indexes between time periods. Changes occurred both over the longer time perspective (1921–1940 vs. 1981–2000) and over the shorter time period comparisons (1921–1940 vs. 1951–1970 and 1951–1970 vs. 1981–2000). The temporal patterns were similar in red-listed and non red-listed species, indicating that both small and large populations were subject to decreases or increases. However, the population dynamic mechanisms seemed to depend on population size, as the *Population Size Index* (PSI) was more closely related to range among rare

species than in common ones (Fig. 5). The mechanisms also differed between increasing and decreasing species – with the ranges of decreasing species being generally unchanged (at the scale of the study) regardless of commonness, i.e. a population thinning. In contrast, increasing species showed corresponding range expansions for rare but not common species. Since most species show a change in relative species range in the spectrum from neutral to expanding, this might indicate rather stable population ranges, or a higher spatial effort in sampling that was not accounted for in our analysis. The species-specific results generally agree well between the model reduction analysis and the hierarchical partitioning, and for the majority of species time and/or relative range were the most important variables, with the number of collectors generally not being as important.

Our expectation was that declining rarer species would exhibit larger range contractions than declining common species, but the results did not support this. One explanation for this is that population density, but not range, has decreased, perhaps because of deteriorating habitat quality or poorer climatic conditions. However, even if a declining species is still present in all of its sub-populations, the risk of local (and ultimately total) extinction risk may be elevated due to lower population density [25]. If there is no clear meta-population structure, we generally expect a more gradual increase in extinction risk, other things equal. Obviously, to evaluate the future prospects of declining longhorn beetles it may be critical to know their population structure, especially among rarer species that can be suspected to be governed by meta-population dynamics. Interestingly, information in the older entomological literature indicates that the perceived range and commonness of many longhorn beetles in Sweden have been remarkably constant over even longer time frames [35], which suggests that even relatively rare species have been able to survive in spite of what appears to be few, fragmented or small populations. An alternative explanation for our results is that range, and possibly density, has decreased for declining species, but at a smaller spatial scale than was used here. If so, the range contraction is scattered, i.e. the species has disappeared from local sites distributed over the entire range of the species. This means that local sub-populations have gone extinct, which could be due to processes linked to small population size or to deteriorating environmental conditions. This type of range contraction would correspond to a decrease in smaller scale area of occupancy (AOO), but not in extent of occurrence (EOO) [26, 30]. However, the current analysis assumes that regional rarity, as total number of records, reflects local rarity, and this is not necessarily the case. A general positive correlation between global and local abundance has often been observed [6, 7], but this might not hold for Swedish longhorn beetles, and empirical data of local commonness is needed to substantiate this assumption. Looking at our data, comparing common-

ness at global and local scales, we find examples of globally common species being locally common (e.g. *Anoplodera sanguinolenta*), but also species that are relatively rare on the global scale being locally common (e.g. *Pyrrhodium sanguineum*) (Jeppsson et al., unpublished). This is, however, still a measure of local commonness at a relatively coarse scale and pooled over time, and not a substitute for estimates of commonness from a standardized inventory.

For increasing species, rare species showed larger range expansions relative to common species; thus supporting the prediction that rarer species expand their range more than increasing common species do. This suggests that common species occupy most available suitable habitat and that increases in population size are caused by higher population density. Rarer species, on the other hand, seemed to occupy suitable existing but vacant areas when populations increase [19, 28]. An alternative explanation for larger range expansions in rarer species is that recent changes in land use or conservation measures have created more suitable habitat, thereby facilitating the range expansion. While possible, this explanation fails to account for why additional suitable habitat has not also been created for the common species to the same extent.

We did not observe larger population declines in species with a larger degree of host specialization, where a negative effect has often been hypothesised [18] or observed (i.e. [11, 40]). However, the number of host species only deals with a small amount of the possible dimensions of specialization. Some larval host trees are also, ignoring other aspects of substrate quality, extremely common, which can make number of host tree species an unreliable predictor of species sensitivity. For instance, some species in this dataset feed exclusively on the two coniferous species Scots Pine (*Pinus sylvestris*) and Norwegian spruce (*Picea abies*) that make up the boreal forests in Sweden, and aspects of substrate coarseness, sun-exposure, moisture and stages of decomposition are most certainly more important for the sensitivity of these species than the number of host tree species that they utilize [16].

4.1 Data evaluation

All trends presented here are conditional on the estimate of sampling effort. Therefore, a main assumption is that the overall number of longhorn beetles, i.e. the sum of the population sizes of all species, has not changed in any direction during our study period. Unfortunately there is no independent measure of the overall trend of longhorn beetles in Sweden, although such information would be the ideal backdrop for evaluating our species-specific trends. However, with the assumption that the overall number of records is a fair description of the abundance of longhorn beetles, there is no evidence for an overall trend as seen from the asymptote in record numbers in the later part of the 20th century (Fig 1a). Three alternatives can

produce this asymptotic curve; a) constant number of longhorn and constant effort, b) decreasing longhorns and increasing effort, or c) increasing longhorns and decreasing effort. We view alternative c) as highly unlikely, as the numbers of collectors and species collected per year has remained more or less the same for decades (Fig 1), and since the biodiversity issue gained influence in the later part of the 20th century, leading to an increased interest in rare species. It is harder to discriminate between alternative a) and b). This means that the overall trend of longhorn beetles is in the spectrum of neutral to decreasing, which corresponds to our species trends being fairly unbiased to biased upwards, so estimates of negative population trends may under-estimate the rates of decline whereas estimates of population increase may be larger than the actual trends. It should also be remembered that the same argument applies to red-listed species, and the analysis assumes that red-listed species do not change in abundance as a group. If we believe that red-listed species are generally declining, then the trends estimated here are underestimations. Furthermore, the estimates of change are conservative in the sense that the number of individuals observed at each collection event is not included in the database, but only represented by a single record. Hence, the database does not differentiate between a collection event where a large number of individuals were observed from one where only a single specimen was found, underestimating the magnitude of change. Since the sampling intensity has increased over time, both for red-listed and non-red-listed species, recent estimates of abundance or range should be more certain than older ones. This would result in declines being underestimated and increases overestimated, especially for range, a conclusion shared by Olden and Poff[44]. It can be argued that the effect of red-listing should only show after the publication of the first red-list in 1986, but the first red-list only confirmed what had already been expressed before, and the identification and focus on later-to-be red-listed species started earlier, as can be seen in the Swedish entomological journal 'Entomologisk tidskrift'. Therefore we chose to model the sampling effort for red-listed species for the entire time period studied, something that is also corroborated by the inflection point of the fitted function.

Theoretically, our measure of effort could be heavily influenced by a couple of species showing strong trends. This would however result in a bimodal distribution of PSI changes, which we did not observe (Fig. 2). The observed excess of large positive changes, especially between the first and the last 20-year-periods, stem from uncommon species that only have a marginal effect on the estimate of sampling effort. Another basic assumption is obviously that changes in the records-based species' frequency reflect actual population changes, but since there are no other trend estimates for Swedish longhorn beetles, this cannot be verified. However, the positive correlation between the number of records for each species

with the red list categorization or with the species' appraisal done by Swedish entomologists (Jeppsson et al. unpublished) suggests that the commonness of species in the database reflect the commonness in the wild.

Clearly, improved methods of collecting specimens and recording species presence, e.g. flight-trapping, hatching of beetles from substrates taken indoors, use of UV lamps for attracting night-active beetles and identification of exit holes, galleries and other traces of beetle activity may significantly increase the probability that certain species are recorded. In this study we controlled for such effects by using only records that refer to handpicked specimens. It is, however, important to remember that for species with a high proportion of records from other collection methods, such as *Nothorhina muricata*, that these records are not taken into account in this study. Similar changes in relative species frequencies in NHCs without corresponding changes in nature may be the result of that certain species are perceived as becoming more – or less – valuable. To evaluate such effects we asked collectors how they value species and compared their ranking of species with a grading system for trading beetles between collectors [2]. The results indicate that declining species have become more, and increasing species less, interesting to collect [35]. For instance, *Agapanthia villosoviridescens*, *Grammoptera ruficornis* and *Leiopus nebulosus* (all increasing) are the three species showing the largest declines in collector appreciation, while *Hylotrupes bajulus* and *Rhagium sycophanta* (both declining) are the two species with the largest increases in appreciation [35]. This suggests that our indices, both positive and negative, generally under-estimate the real population trends. To summarize the discussion of possible biases; even though independent estimates of species trends would be desirable to evaluate our results against, after reviewing the evidence, we argue that our estimates of PSI are not flawed. We have constructed a species-adjusted measure of sampling effort, which takes red-list status and distribution into account. Naturally, an explicit species-specific estimate of sampling effort would be preferable, but such data are just not available.

Another factor that may influence the collecting probabilities is new knowledge related to species habitats and biology, and this is not taken into account in this study. However, such aspects are mostly relevant for extremely rare species that we did not analyse anyway due to the scarcity of records. Finally, the fact that the measure of relative species range is not independent from the number of records may interfere with the analysis for some species. However, since we do not have an independent measure of species range, there is no way around this problem. Rather, it serves to illustrate that fundamentally, the attributes of population size and population range cannot be entirely separated, since a larger range will also equate to a larger overall population, holding other factors such as density constant.

4.2 Practical applications

The present results can help to guide and complement the red-listing process, in broadening the data source to be used for the red list evaluation process. As the discussion of biases have shown, the levels of decline are not likely to be exaggerated, but rather the opposite, so from a conservation perspective estimates of consistent negative trends should be taken seriously. Currently, with the general deficit of population trend data, all of the red-listed Swedish longhorn species are listed under red-list criteria B or C [23], which mainly evaluate small geographical range or small population size, criteria that are based on meta-population ecology and conservation genetics [39]. We believe that studies like this one can supplement the evaluation of species' conservation status, as well as making it possible to evaluate the species against particularly the red list criterion A, i.e. decline in population size, to a larger extent. When using PSI to evaluate the species analysed here, seven species meet the criteria for VU or NT, and another seven show declines of more than 5 % over 10 years. Only 4 out of these 14 species are currently red-listed (*Chlorophorus herbstii*, *Mesosa nebulosa*, *Prionus coriarius*, *Rhagium sycophanta*), and one has been red-listed earlier (*Oplosia cinerea*). It should be emphasised that many red-listed species are not analysed in this study since they occur at very low frequencies in the database, and that our study should not be used to evaluate the precision of the Red List. Therefore, we believe that this type of analysis of NHC data is most useful for identifying declines in less rare species.

Another finding with practical implications for evaluating species' status was that relative ranges of declining species, irrespective of perceived population size, did not decrease. Thus, if the status of these populations were to be evaluated only from knowledge of changes in their distribution, the declines would have been overlooked, at least at the scale of study used here. In fact, since collectors have become more mobile in recent times, leading to more intensive spatial sampling, this may even produce the false impression that decreasing species are increasing in area of distribution. Consequently, information on distribution changes must be used with great caution as a tool for identifying increasing or declining species.

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