

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

The use of ecological traits in extinction risk assessments: A case study on geometrid moths

Niina Mattila^{a,*}, Janne S. Kotiaho^{a,b}, Veijo Kaitala^c, Atte Komonen^d

^aDepartment of Biological and Environmental Science, P.O. Box 35, FI-40014, University of Jyväskylä, Finland

^bNatural History Museum, P.O. Box 35, FI-40014, University of Jyväskylä, Finland

^cDepartment of Biological and Environmental Science, P.O. Box 65, FI-00014, University of Helsinki, Finland

^dFaculty of Forest Sciences, P.O. Box 111, FI-80101, University of Joensuu, Finland

ARTICLE INFO

Article history:

Received 25 February 2008

Received in revised form

22 May 2008

Accepted 27 June 2008

Available online 9 August 2008

Keywords:

Extinction risk

Geometridae

IUCN criteria

Predictive conservation science

ABSTRACT

Identifying ecological traits that make some species more vulnerable than others is vital for predictive conservation science. By identifying these predisposing traits we can predict which species are most prone to decline and gain an understanding of the reasons behind the decline. The aim of this study was to determine the ecological traits that best predict extinction risk and distribution change in Finnish geometrid moths and to develop an understanding of the biological connections between these traits and threats. We found that larval specificity, overwintering stage and flight period length predicted distribution change and extinction risk. There was also an interaction effect between larval specificity and body size on both distribution change and extinction risk. In monophagous species the host plant distribution predicted extinction risk. Even though ecological traits are known to be important determinants of extinction risk, the IUCN red list categorization system is exclusively based on quantitative measures of populations and ignores the ecological traits. Here, we propose that taxon specific ecological data should also be used to predict extinction risk at least on a regional scale to improve the accuracy of the IUCN extinction risk classification.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

Anthropogenic habitat loss and climate change are the greatest threats to biological diversity (Pimm et al., 1995; Chapin et al., 2000; Novacek and Cleland, 2001; Warren et al., 2001; Thomas et al., 2004). It is important to note, however, that some species seem to be more vulnerable to these external threats than others. Indeed, not all species have declined and the risk of extinction is not evenly distributed among taxa (Bennett and Owens, 1997; Purvis et al., 2000; Jones et al., 2003). The main reason for the uneven distribution of extinction risk is likely to be that the intrinsic ecological traits

of a species determine how well it is able to withstand the threats to which it is exposed (Cardillo et al., 2004). One of the primary goals of conservation biology should indeed be to gain an understanding of the ecological traits that predispose species to population decline, range contraction, and eventually to extinction (Pimm et al., 1988; Caughley, 1994). We believe that identifying the traits that are shared by species that are known to have declined, and thus at risk of extinction, will help us to gain this understanding and to predict, which species are at the greatest risk of becoming extinct already before they become threatened. Having this ability, we would be able to be proactive and initiate the

* Corresponding author.

E-mail addresses: niimatt@cc.jyu.fi (N. Mattila), janne.kotiaho@bytl.jyu.fi (J.S. Kotiaho), veijo.kaitala@helsinki.fi (V. Kaitala), atte.komonen@joensuu.fi (A. Komonen).

0006-3207/\$ - see front matter © 2008 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2008.06.024

necessary measures for conservation of species when their populations are still viable instead of reacting only to the imminent extinction risk when it already may be too late.

Determinants of species' vulnerability have been studied by comparing ecological traits of species classified as threatened and unthreatened (e.g. Jones et al., 2003; Cardillo et al., 2004; Kotiaho et al., 2005), but also by examining the ecological traits that correlate with distribution change (e.g. Warren et al., 2001; Mattila et al., 2006). However, ecological traits that are correlated with extinction risk may be different from those correlated with distribution change (Mattila et al., 2006). Therefore, to gain a solid basis for predictions of which species are most vulnerable, studies focussing simultaneously on both are needed.

In this study we determine the ecological traits that correlate with both distribution change and extinction risk in 284 species of Finnish geometrid moths (Geometridae). We base our measure of extinction risk on the World Conservation Union (IUCN) risk of extinction categories (Rassi et al., 2001). In general, the IUCN extinction risk classification is based on quantitative measures, i.e. population size, range size and decline in these. In addition to presenting new empirical data, we suggest that IUCN should incorporate the ecological traits that are known to predispose species to extinctions, in to the classification criterion.

2. Materials and methods

2.1. Distribution change

Of the 302 geometrid moth species that occur in Finland, we included in our study the 284 species that have a permanent population in Finland (Huldén et al., 2000). Distribution change is based on the "Atlas of Finnish Macrolepidoptera" (Huldén et al., 2000), which gives the distribution in Finland as the number of occupied 10 × 10 km grid cells in the national coordinate system. This atlas covers all reliable records and observations from 1747 to 1997. Reliable means that there must be a published record of the observation or that there is a conserved specimen in some museum of private collection. The distribution data in the atlas are divided in observations before 1988 and observations between 1988 and 1997. The difference in these distributions, i.e. in the number of occupied 10 × 10 km grid cells, was used to estimate the distribution change for each species. Even though these two time periods are unequal, the earlier period being much longer, there were still more observations recorded during the later period (Huldén et al., 2000). We acknowledge that it is possible that the inequality of the time periods and the difference in observation activity may bias the overall magnitude of the distribution change. However, this bias is unlikely to explain our main findings i.e. that the ecological traits correlate with the distribution change. There is unlikely to be any comprehensive or single mechanism for why the possible bias should correlate with the ecological traits. Further critique and problems about the use of atlas data in general can be found e.g. from the work of Dennis and colleagues (1986, 1999) and for this particular atlas data from our previous work (Mattila et al., 2006).

2.2. Threatened and unthreatened species

We classified moth species into two categories: threatened ($n = 31$) and unthreatened ($n = 253$). This distinction was based on IUCN risk of extinction categories (IUCN, 2001). We classified near threatened, vulnerable, endangered and critically endangered species as threatened. Species of least concern were included in the unthreatened category. We considered threatened species as being at risk of extinction whereas unthreatened species were not considered to be at risk. The principal determinant of the IUCN extinction risk class for geometrid moths in Finland is the area of occupancy (Rassi et al., 2001). Also decline of the distribution is used and as a consequence distribution change may correlate with extinction risk.

2.3. Ecological traits

The ecological traits we analyzed were body size, larval host plant specificity, larval host plant distribution, length of flight period, and overwintering stage. The average body size (wing span) was a mean measured from 25 individuals (mm; \log_{10} -transformed; Mikkola et al., 1985, 1989) and for some rare species from fewer individuals. In our analyses we used male size to include species with wingless females. This does not have any effect on our results, because there is a very strong correlation between male and female body size (Pearson correlation, $r = 0.97$, $n = 264$, $p < 0.001$; species with wingless females were excluded). Species were divided into three categories based on larval host plant specificity: monophagous species use only one host plant species, oligophagous species use plants in one genus and the others are polyphagous. Data on larval host plants were based on Mikkola et al. (1985, 1989) and Huldén et al. (2000). For the monophagous species the larval host plant distribution was measured as the number of occupied 10 × 10 km grid cells in the Finnish national coordinate system. This host plant distribution data were based on the national floristic database (Lahti et al., 1995). The length of flight period was defined as being the average number of days the adults have been seen on flight (Mikkola et al., 1985, 1989). If the species has more than one generation per year, only the flight period length of the first generation was used. This is because the second generation is often facultative. Overwintering stages applied were egg, larva or pupa (Huldén et al., 2000). Our data comprised no geometrid species that overwinter as an adult. Note that some traits have not been documented for all species; hence the sample size may vary between analyses.

2.4. Phylogeny

Evolutionarily closely related species tend to share many characters through common descent rather than through independent evolution. Thus, statistical methods that treat such characters as independent may be problematic (Harvey and Pagel, 1991; Harvey and Purvis, 1991). The method of independent contrasts can be applied to use phylogenetic information to transform interspecific data into values that can be analyzed with standard statistical methods (Harvey and Pagel, 1991; Purvis and Rambaut, 1995). However, if a

phylogeny is not properly resolved, as is the case in geometrid moths, any correction based on it will be incorrect. Moreover, what is often not recognized is that there are a few rather strict assumptions that must be met before the phylogenetically independent contrasts are in fact phylogenetically independent and the method can fail if the data is not correctly transformed prior to the analysis (Freckleton, 2000). If the assumptions cannot be met one cannot rely on the results from phylogenetic corrections. For these reasons, we derive our results from the original species data without correcting for phylogeny. Statistical analyses were conducted in SPSS (version 13.0 for Windows; SPSS, Chicago, IL, USA).

3. Results

3.1. Distribution change

Overall, the distribution of geometrid moths declined 21.5% between the two time periods (one sample t-test against 0, $t = -10.04$, $df = 282$, $p < 0.001$). The distribution of threatened species declined on average 45.7% whereas the distribution of unthreatened species declined on average 18.5%. The difference in the distribution change between these groups was significant (independent samples t-test, $t = 4.09$, $df = 281$, $p < 0.001$).

To analyze the relationship between the distribution change and species specific ecological traits, we entered larval specificity, body size, length of the flight period and overwintering stage simultaneously into an analysis of covariance (ANCOVA). We began by entering all main effects and two-way interactions into the model, followed by stepwise removal of nonsignificant interactions. All of the ecological traits but body size had a significant effect on the distribution change (Table 1). Regarding larval specificity, monophagous species had declined more than oligophagous (LSD test, $MD = -11.92$, $\pm SE = 4.75$, $p = 0.013$) or polyphagous species (LSD test, $MD = -10.43$, $\pm SE = 4.31$, $p = 0.016$). There was no difference between oligo- and polyphagous species (LSD test, $MD = 1.49$, $\pm SE = 3.23$, $p = 0.645$). There was also an interesting interaction effect between larval specificity and body size (Table 1): in monophagous species larger species had declined more than smaller species, and in polyphagous species smaller species had declined more than larger species (Fig. 1). Within monophagous species we also analyzed the effect of host plant distribution but it did not predict the distribution change (linear regression, $F = 1.42$, $df = 36$, $p = 0.241$, $R^2 = 0.04$).

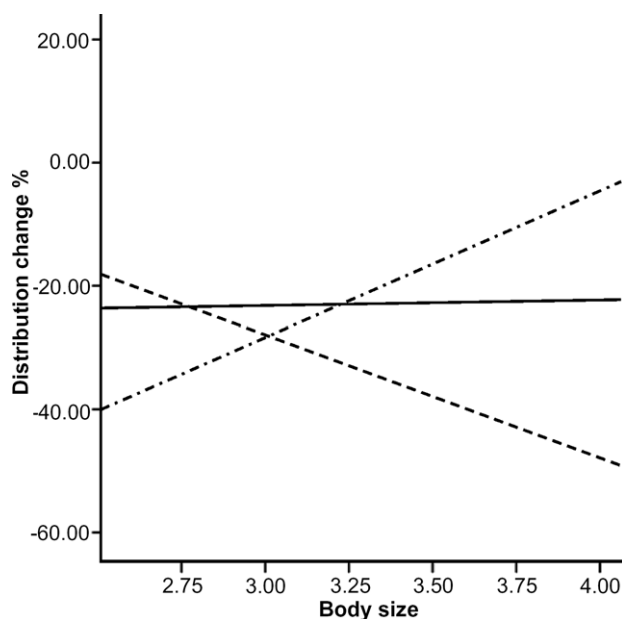


Fig. 1 – Distribution change (%) of geometrid moths in relation to body size. Dash line represents monophagous species, continuous line represents oligophagous species and dash-dot polyphagous species.

Overwintering stage had an effect on distribution change such that species overwintering as egg had declined less than species overwintering as larva or pupa (LSD test, $MD = 12.60$, $\pm SE = 4.22$, $p = 0.003$ and $MD = 10.10$, $\pm SE = 3.83$, $p = 0.009$, respectively). There was no difference in distribution change between species overwintering as larva or pupa (LSD test, $MD = -2.50$, $\pm SE = 3.23$, $p = 0.440$). Species with shorter flight period had declined more than species with longer flight period (ANCOVA, parameter estimate $B = 0.41$, $SE = 0.16$, $t = 2.57$, $p = 0.011$).

3.2. Risk of extinction

To analyze the effects of ecological traits on the extinction risk we entered larval specificity, body size, length of the flight period and overwintering stage simultaneously into a logistic regression. We began by entering all main effects and two-way interactions into the model followed by a stepwise removal of the nonsignificant interactions. The final model was significant (logistic regression, $\chi^2 = 47.23$, $df = 8$, $p <$

Table 1 – Analysis of covariance of the effects of ecological traits on distribution change of geometrid moths

Source	df	MS	F	p	η^2
Overwintering stage	2	2245.45	4.79	0.009	0.036
Larval specificity	2	2405.78	5.13	0.007	0.038
Body size	1	3.27	0.01	0.934	<0.001
Flight period length	1	3087.41	6.58	0.011	0.025
Larval specificity* Body size	2	2627.14	5.60	0.004	0.042
Error	257	469.01			

* $R^2 = 0.13$.

0.001, Nagelkerke $r^2 = 0.32$), and all of the ecological traits but overwintering stage had a significant effect on the risk of extinction (Table 2). Although not quite significant, the overwintering stage also tended to have an effect (Table 2). Regarding larval specificity, monophagous species had a greater risk of extinction than polyphagous species (logistic regression, $B = -18.77$, $SE = 7.36$, $Wald = 6.50$, $df = 1$, $p = 0.011$) but there was no difference between oligophagous and polyphagous species or between oligophagous and monophagous species ($B = 2.02$, $SE = 9.32$, $Wald = 0.05$, $df = 1$, $p = 0.829$ and $B = 16.75$, $SE = 10.76$, $Wald = 2.42$, $df = 1$, $p = 0.120$, respectively). There was also an interaction effect between larval specificity and body size on risk of extinction (Table 2) such that in monophagous species larger species were more often threatened than smaller species, while in oligophagous and polyphagous species the trend with body size did not exist or if anything was reversed (Fig. 2). Within monophagous species there was also a negative relationship between distribution of host plant species and the risk of extinction (logistic regression, $\chi^2 = 6.92$, $df = 1$, $p = 0.009$, Nagelkerke $r^2 = 0.25$).

Species overwintering as larva tended to have a greater extinction risk than species overwintering as egg (logistic regression, $B = -1.61$, $SE = 0.84$, $Wald = 3.68$, $df = 1$, $p = 0.055$). Species overwintering as egg or larva did not differ from those overwintering as pupa ($B = 0.79$, $SE = 0.80$, $Wald = 0.95$, $df = 1$, $p = 0.326$ and $B = -0.83$, $SE = 0.53$, $Wald = 2.43$, $df = 1$, $p = 0.119$, respectively). Flight period length had an effect such that species with shorter flight period length had a greater extinction risk ($B = -0.17$, $SE = 0.039$, $Wald = 17.94$, $df = 1$, $p < 0.001$).

4. Discussion and conclusions

The distribution of threatened species had declined more than that of unthreatened species. Larval specificity, overwintering stage and flight period length predicted distribution change and extinction risk. There was also an interaction effect between larval specificity and body size on both distribution change and extinction risk. In monophagous species the host plant distribution was not related to distribution change but it nevertheless predicted extinction risk.

Ecological traits in relation to distribution change and extinction risk

4.1. Overwintering stage

Overwintering stage of geometrids was related to distribution change and tended to be related to extinction risk although the latter relationship was not quite significant. Our results

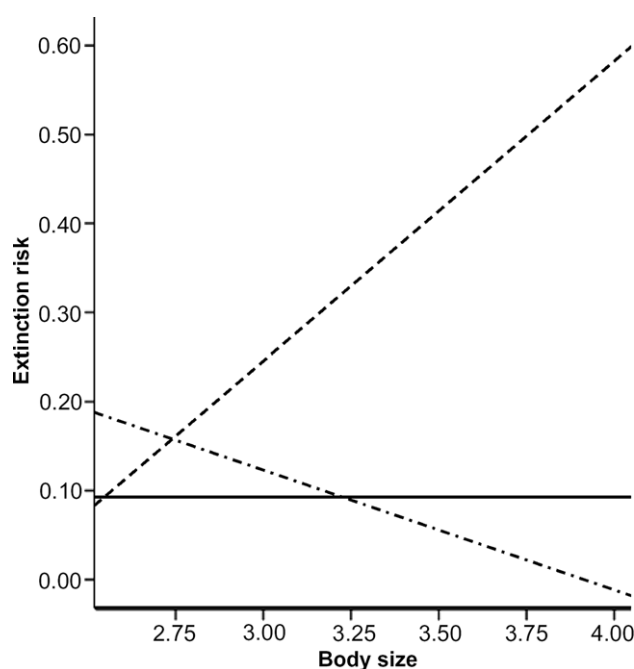


Fig. 2 – Extinction risk of geometrid moths in relation to body size (ln). Dash line represents monophagous species, continuous line represents oligophagous species and dash-dot polyphagous species.

agree with the data from 306 species of Finnish noctuid moths in which overwintering stage was the only trait that predicts distribution change (Mattila et al., 2006). It is worth noting that the climate in Finland may be rather restrictive, as Finland rests completely above the 60 degrees of northern latitude, and snow cover often lasts from the end of November to early April. Overwintering stage is related to climate such that across Finland there is a gradual change of the overwintering stages over the latitudinal gradient (Virtanen and Neuvonen, 1999). In the north, species overwinter mostly as larvae but the incidence of overwintering in other stages increases toward the south (Virtanen and Neuvonen, 1999). Hence, it is likely that the distribution of lepidopterans in Finland may be determined by climatic factors affecting differentially species with different life histories: eggs are more prone to cold winter temperatures because egg overwinterers commonly feed and overwinter on trees (Virtanen and Neuvonen, 1999). Eggs on trees are not covered by insulating snow cover and may thus benefit from warming climate, whereas at the same time thinning snow cover may decrease the overwintering success of pupae and larvae stages that are usually

Table 2 – Logistic regression on the risk of extinction of geometrid moths

Effect	-2 log likelihood	χ^2	df	p
Overwintering stage	143.70	4.90	2	0.087
Larval specificity	146.29	7.49	2	0.024
Body size	138.81	0.00	0	
Flight period length	164.93	26.12	1	<0.001
Larval specificity*	147.68	8.88	2	0.012
Body size				

covered by snow. In addition, because of their life history, egg over winterers tend to fly late in the summer or in the autumn and benefit from warm long autumn. Perhaps our finding, that in the geometrid moths the egg over winterers have declined the least, may be explained by their above mentioned life history and the current climate change.

4.2. Resource specificity

Larval host plant specificity was a significant predictor of both distribution change and risk of extinction. It seems that there is a very clear pattern emerging among lepidoptera in general (Koh et al., 2004; Kotiaho et al., 2005; Mattila et al., 2006; Mattila et al., unpublished); more specialized species are at a greater risk of extinction than other species. Interestingly, the distribution of large monophagous species had declined more, and they were more threatened than smaller monophagous species. Monophagous species are in general smaller than polyphagous species in geometrid and noctuid moths (Niemi et al., 1981; Lindström et al., 1995). The same trend has also been observed among British macrolepidoptera (Loder et al., 1998). Several mechanisms have been put forward to explain the connection between body size and feeding specialization (e.g. Lindström et al., 1995), but no conclusive support for any of the mechanisms has been found (Loder et al., 1998). Unravelling the mechanism that causes this relationship remains an important objective for future research. However, even if we do not yet understand the underlying reasons, it seems that monophagous species are indeed at greater risk of extinction than other species, and body size is an important determinant of how well monophagous species are able to withstand the threats.

In monophagous species host plant distribution predicted extinction risk but not distribution decline. These same results were found also in noctuid moths (Mattila et al., 2006). The host plant distribution sets a limit on the distribution of insect species living on them and small host plant distribution ineluctably means small distribution for the dependent species. The fact that the distribution is the principal determinant of extinction risk classification in geometrid moths, is likely to be the causative factor behind the correlation between the distribution of host plant and the extinction risk of the moths.

4.3. Flight period length

Geometrid species with shorter flight period length have declined more and were also more often threatened. Flight period length predicted extinction risk also in butterflies (Kotiaho et al., 2005) and in noctuid moths (Mattila et al., 2006), although it did not predict distribution decline in these species (Mattila et al. unpublished, Mattila et al., 2006). It has been observed that species closer to the northern edge of their geographical range have shorter flight period than species further away from the edge (Komonen et al., 2004). Populations of these edge species tend to inhabit only the best quality patches (Hanski, 1999) and have also lower dispersal ability (Komonen et al., 2004). Together the limited number of suitable habitat patches and lower dispersal ability are

probably the factors that predispose species with short flight period to distribution decline and extinction risk.

4.4. IUCN risk assessing system and ecological traits

Most countries have legislation that obliges them to identify and protect threatened species. Numerous systems have been devised to assess levels of extinction risk faced by species, but most of them are used only locally or on a limited number of taxa (Millsap et al., 1990). The most widely recognized system for assessing extinction risk is the IUCN red list categorization system that was first developed to assess extinction risk at the global level (IUCN, 2003). This system has become a conservation cornerstone in many countries, and has increasingly been used as a tool in assessing extinction risk and conservation priorities (Keller and Bollman, 2004). IUCN has encouraged this by publishing guidelines for national and regional use (IUCN, 2003). However, IUCN extinction risk assessments are exclusively based on quantitative data of the observed abundance, distribution and distribution decline which are mostly only secondary phenomena, i.e. the response of the species to the threats. Indeed, IUCN risk assessment system ignores ecological traits that directly contribute to the vulnerability in the first place. Although a few other categorization systems, in which ecological traits can be included, have been described (e.g. Millsap et al., 1990; Ceballos and Navarro, 1991; Cofré and Marquet, 1999), the lack of ecological traits in the IUCN risk assessment system may be seen as a problem because of its globally prominent status. The use of the knowledge of predisposing ecological traits would produce more specific extinction risk assessments. However, the aim of the IUCN red list is also to be internationally comparable and thus national applications do not give opportunity to make new, ecological criteria to increase the accuracy of IUCN extinction risk assessments. Ecological traits can, and are encouraged to, be taken into account in conservation management (IUCN, 2003), but the classification status of species has an important influence on the allocation of resources for conservation and it also often determines whether there is a need for legal or other protection of species and their habitats. We argue that it is always advisable to take ecological traits into account whenever such data are available.

The IUCN extinction risk cannot always be defined due to the lack of quantitative data on populations even though species' biology may be well known (Rassi et al., 2001). This lack of information is especially prevalent in developing countries into which most of the global diversity is concentrated (Myers et al., 2000) and in which risk assessments are urgently needed. In such a case, even a coarse estimation of extinction risk may be a better alternative than only giving species a label "data deficient". Here ecological traits could be used as a substitute for the absent quantitative population data. It may be a problem that all predisposing traits are not likely to be universal even among the same group of organisms. This is because the threatening factors as well as ecological and environmental factors vary between geographical areas. For example among common British macro-moths, species overwintering as eggs have declined the most (Conrad et al., 2004) whereas for noctuid (Mattila et al., 2006) and geometrid

moths in Finland, species overwintering as eggs have fared the best. Therefore, some ecological traits can only be used on smaller geographical scale to improve the accuracy of regional extinction risk assessments. Nevertheless, for some traits global patterns can be found: there is now clear evidence that ecological specialization, be it for example on diet or habitat breadth, is an important determinant of extinction risk not only in lepidopterans (Koh et al., 2004; Kotiaho et al., 2005; Mattila et al., 2006) but also in many other groups of animals, e.g. in mammals (Haracourt et al., 2002; Boyles and Strom, 2007), in reptiles (Foufopoulos and Ives, 1999), in fishes (Angermeier, 1995) and in birds (Julliard et al., 2003; Shultz et al., 2005; Cofré et al., 2007). These kinds of traits that have ample empirical support to be globally predisposing species to distribution decline and extinction should be included in the IUCN risk assessing criteria.

Acknowledgements

We thank the “Monday coffee club” members and Miska Luoto and Jussi Päivinen for their valuable comments and contributions on the manuscript. We are also grateful to R. Lampinen and A. Kurtto for numerical data on the distribution of plants. This study was supported by the Academy of Finland and by the Center of Excellence In Evolutionary Research.

REFERENCES

- Angermeier, P.L., 1995. Ecological attributes of extinction prone species: loss of freshwater fishes in Virginia. *Conservation Biology* 9, 143–158.
- Bennett, P.M., Owens, I.P.F., 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceedings of the Royal Society of London Series B* 264, 401–408.
- Boyles, J.G., Strom, J.J., 2007. The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. *PLoS ONE* 2 (7), e672.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J., Mace, G.M., 2004. Human population density and extinction risk in the world's carnivores. *PLoS Biology* 2, e197.
- Caughley, G., 1994. Directions in conservation biology. *Journal of Animal Ecology* 63, 215–244.
- Ceballos, G., Navarro, D., 1991. Diversity and conservation of Mexican mammals. In: Mares, M.A., Schmidly, D.J. (Eds.), *Latin American mammalogy: history, diversity and conservation*. University of Oklahoma Press, Norman, pp. 167–198.
- Chapin III, F., Zavaleta, E., Eviner, V., Naylor, R., Vitousek, P., Reynolds, H., Hooper, D., Lavorel, S., Sala, O., Hobbie, S., et al., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- Cofré, H.L., Marquet, P.A., 1999. Conservation status, rarity, and geographic priorities for conservation of Chilean mammals: an assessment. *Biological Conservation* 88, 53–68.
- Cofré, H.L., Böhning-Gaese, K., Marquet, P.A., 2007. Rarity in Chilean forest birds: which ecological and life-history traits matter. *Diversity and Distributions* 13, 203–212.
- Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R., Warren, M.S., 2004. Long-term population trends in widespread British moths. *Journal of Insect Conservation* 8, 119–136.
- Dennis, R.L.H., Williams, W.R., 1986. Butterfly diversity. Regressing and a little latitude. *Antenna* 10, 108–112.
- Dennis, R.L.H., Sparks, T.H., Hardy, P.B., 1999. Bias in butterfly distribution maps: the effects of sampling effort. *Journal of Insect Conservation* 3, 33–42.
- Foufopoulos, J., Ives, A.R., 1999. Reptile extinctions on land-bridge islands: life history attributes and vulnerability to extinction. *American Naturalist* 153, 1–25.
- Freckleton, R.P., 2000. Phylogenetic tests of ecological and evolutionary hypotheses: checking for the phylogenetic independence. *Functional Ecology* 14, 129–134.
- Hanski, I., 1999. *Metapopulation ecology*. Oxford University Press, Oxford.
- Haracourt, A.H., Coppeto, S.A., Parks, S.A., 2002. Rarity, specialization and extinction in primates. *Journal of Biogeography* 29, 445–456.
- Harvey, P.H., Pagel, M.D., 1991. *Comparative method in evolutionary biology*. Oxford University Press, Oxford, United Kingdom.
- Harvey, P.H., Purvis, A., 1991. Comparative methods for explaining adaptations. *Nature* 351, 619–624.
- Huldén, L., Albrecht, A., Itämies, J., Malinen, P., Wettenhovi, J., 2000. *Atlas of Finnish Macrolepidoptera*. Lepidopterological Society of Finland, Finnish Museum of Natural History, Helsinki.
- IUCN (World Conservation Union), 2001. *IUCN red list categories*. Version 3.1. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- INCN, 2003. *Guidelines for application of IUCN red list criteria at regional levels: Version 3.0*. IUCN species survival commission, IUCN. Gland, Switzerland and Cambridge, United Kingdom.
- Jones, K.E., Purvis, A., Gittleman, J.L., 2003. Biological correlates of extinction risk in bats. *American Naturalist* 161, 601–614.
- Julliard, R., Jiguet, F., Couvet, D., 2003. Common birds facing global changes: what makes a species at risk? *Global Change Biology* 10, 148–154.
- Keller, V., Bollman, K., 2004. From red list to species of conservation concern. *Conservation Biology* 18, 1636–1644.
- Koh, L.P., Sodhi, N.S., Brook, B.W., 2004. Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology* 18, 1571–1578.
- Komonen, A., Kaitala, V., Kotiaho, J.S., Päivinen, J., 2004. The role of niche breadth, resource availability and range position on the life history of butterflies. *Oikos* 105, 41–54.
- Kotiaho, J.S., Kaitala, V., Komonen, A., Päivinen, J., 2005. Predicting the risk of extinction from shared ecological characteristics. *Proceedings of the National Academy of Sciences of the United States of America* 102, 1963–1967.
- Lahti, T., Lampinen, R., Kurtto, A., 1995. *Atlas of the Distribution of Vascular Plants in Finland*. University of Helsinki, Finnish Museum of Natural History and Botanical Museum, Helsinki.
- Lindström, J., Kaila, L., Niemelä, P., 1995. Polyphagy and adult body size in geometrid moths. *Oecologia* 98, 130–132.
- Loder, N., Gaston, K.J., Warren, P.H., Arnold, H.R., 1998. Body size and feeding specificity: macrolepidoptera in Britain. *Biological Journal of the Linnean Society* 63, 121–139.
- Mattila, N., Kaitala, V., Komonen, A., Kotiaho, J.S., Päivinen, J., 2006. Ecological determinants of distribution decline and risk of extinction in moths. *Conservation Biology* 20, 1161–1168.
- Mikkola, K., Jalas, I., Peltonen, O., 1985. *Suomen perhoset, Geometroidea 1*. Suomen Perhostutkijain Seura, Helsinki.
- Mikkola, K., Jalas, I., Peltonen, O., 1989. *Suomen perhoset, Geometroidea 2*. Suomen Perhostutkijain Seura, Helsinki.
- Millsap, B.A., Gore, J.A., Runde, D.E., Cerulean, S.I., 1990. Setting the priorities for the conservation of fish and wildlife species in Florida. *Journal of Wildlife Management* 54, 5–57. *Wildlife Monographs Supplement*.

- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Niemelä, P., Hanhimäki, S., Mannila, R., 1981. The relationship of adult size in noctuid moths (Lepidoptera, Noctuidae) to breadth of diet and growth form of host plants. *Annales Entomologici Fennici* 47, 17–20.
- Novacek, M., Cleland, E., 2001. In: *The current biodiversity extinction event: scenarios for mitigation and recovery*, vol. 98. *Proceedings of the National Academy of Sciences, USA*. 5466–5470.
- Pimm, S.L., Jones, H.L., Diamond, J., 1988. On the risk of extinction. *American Naturalist* 132, 757–785.
- Pimm, S., Russell, G., Gittleman, J., Brooks, T., 1995. The future of biodiversity. *Science* 269, 347–350.
- Purvis, A., Rambaut, A., 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applications in the Biosciences* 11, 247–251.
- Purvis, A., Agapow, P.M., Gittleman, J.L., Mace, G.M., 2000. Nonrandom extinction and the loss of evolutionary history. *Science* 288, 328–330.
- Rassi, P., Alanen, A., Kanerva, T., Mannerkoski, I., 2001. *The 2000 Red List of Finnish Species*. Ministry of the Environment and Finnish Environment Institute, Helsinki.
- Shultz, S., Bradbury, R.B., Evans, K.L., Gregory, R.D., Blackburn, T.M., 2005. Brain size and resource specialization predict long-term population trends in British birds. *Proceedings of the Royal Society B: Biological Sciences* 272, 2305–2311.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend-Peterson, A., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Virtanen, T., Neuvonen, S., 1999. Climate change and macrolepidopteran biodiversity in Finland. *Global Change Science* 1, 439–448.
- Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D., Thomas, C.D., 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414, 65–69.