Ann. Zool. Fennici 40: 71–80 ISSN 0003-455X
Helsinki 30 April 2003 © Finnish Zoological and Botanical Publishing Board 2003

Understanding the ecology of extinction: are we close to the critical threshold?

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Received 25 Nov. 2002, revised version received 20 Jan. 2003, accepted 21 Jan. 2003

Benton, T. G. 2003: Understanding the ecology of extinction: are we close to the critical threshold? — *Ann. Zool. Fennici* 40: 71–80.

How much do we understand about the ecology of extinction? A review of recent literature, and a recent conference in Helsinki gives a snapshot of the "state of the art"*. This "snapshot" is important as it highlights what we currently know, the tools available for studying the process of extinction, its ecological correlates, and the theory concerning extinction thresholds. It also highlights that insight into the ecology of extinction can come from areas as diverse as the study of culture, the fossil record and epidemiology. Furthermore, it indicates where the gaps in knowledge and understanding exist. Of particular note is the need either to generate experimental data, or to make use of existing empirical data — perhaps through meta-analyses, to test general theory and guide its future development.

Introduction

Few would argue that managing natural populations and their habitats is one of the greatest challenges for humans in the 21st century. Some species require that management be targeted at them to manipulate their persistence, typically because they are economically important (e.g. harvested, or pest species) or politically important (e.g. "headline conservation" species). More generally, it is important for a number of reasons to manage biodiversity. For example, it can be argued that conserving biodiversity may ensure ecosystem function, is ethically important, is aesthetically pleasing, and safeguards the possibility of future exploitation. Understanding the processes that lead to population persistence, or its flipside, extinction, is therefore an enormous challenge for ecologists. According to the IUCN's 2002 Red List, a total of 11 167 species are currently known to be threatened (http://www.redlist.org/info/tables/table1.html), though this is a gross underestimate of the true value, as, for example, the status of most terrestrial invertebrates is poorly known. Considering birds and mammals, where the status information is more readily available, some 16% of all species are threatened (2329 out of 14 709).

The scientific study of extinction, and the processes that drive it, is one that has been a focus of scientific study over recent decades. However, in comparison with other areas of ecology it has not been as intensely studied (for example, a Web of Science keyword search for the period 1981–2002 indicates that there are about 4 times more papers with keywords "life history and population" than "extinction and population and conservation": 4079 to 992). One catalyst

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* Extinction Thresholds, organised by the Spatial Ecology Programme at the University of Helsinki, held in Helsinki 2–5 September 2002

for studing extinction has been the realisation that populations exist in a spatial context, and global persistence is the result of processes happening at a smaller scale. The study of models of such metapopulations shows that there are often thresholds and non-linearities in their extinction behaviour. In deterministic models, an *extinction threshold* occurs when a marginal change in some parameter (such as habitat fragmentation) causes a change in the probability of extinction from close to zero to close to one. As such, the concept bears much in relation to the proverbial camel, whose back was broken when loaded with an extra wisp of straw. The term "extinction threshold" was coined by Lande (1987), though the existence of threshold behaviour in spatially-implicit Levins-type population models had been evident from Levin's (1969) initial work and had been previously discussed by, amongst others, Hanski (1985). Extinction threshold behaviour was later examined in the spatially explicit metapopulation model of Bascompte and Sole (1996), and has since been found to be a general property in a range of different model formalisations. The extinction threshold is determined by a number of factors, notably the demography of the organism (especially its reproductive rate), the rate at which it disperses across the habitat, the pattern of the habitat in space (especially the fragmentation), and the survival of organisms in the non-habitat environment (the "matrix") (Fahrig 2001).

The study of extinction thresholds has largely been driven by theory. Many approaches have involved numerical investigation, because, until recently, analytical results required an assumption of uniform distributions of habitat over space. Recently, however, analytical approaches have been developed which greatly allow the generality of the extinction threshold concept to be elucidated. One approach is spatially realistic metapopulation theory (Hanski & Ovaskainen 2000, Hanski 2001, Ovaskainen & Hanski 2003). This body of theory includes two main techniques. One is based on a spatial matrix model, with the matrix describing the effect of the landscape on population colonisations and extinctions. As with standard matrix models (Caswell 2001), the dominant eigenvalue describes the population growth rate, and, if it goes below 1.0 the population goes deterministically extinct. The second technique uses "pair approximation" methods that allow the effects of spatial structure in habitat loss on equilibrium metapopulation size and extinction threshold (Ovaskainen *et al.* 2002). In contrast to deterministic theory, stochastic metapopulation theory is now being developed (Frank & Wissel 2002, Ovaskainen & Hanski 2003). The major conceptual change this has on the extinction threshold is that, in the stochastic case, extinction is not only always possible, but in the long-run, almost sure; so instead of a threshold below which the population becomes deterministically extinct, one can consider time to extinction and find the thresholds below which extinction by the specified time becomes highly probable. These different approaches make quite different assumptions, but they draw similar broad conclusions, which emphasise the generality of the results.

Alongside theoretical advances in the study of extinction thresholds, go conceptual ones. An important conceptual advance is the concept of the "extinction debt". Extinction of a population (whether a single population in a patch, or a metapopulation) is a stochastic process, so it is possible for habitat fragmentation to have occurred on a faster timescale than the extinction processes. Thus, populations may be sufficiently fragmented to prevent re-colonisation when they do go extinct — there is therefore a "debt" of extinctions to be paid as a consequence of past habitat loss (Tillman *et al.* 1994, Hanski & Ovaskainen 2002). The concept of debt can be extended beyond that due to habitat loss, *per se*. For example, if there are extinctions then mutually dependent species may be driven extinct, even if the habitat remains hospitable (as may occur to a plant when a seed disperser goes extinct: Pacheco & Simonetti 2000).

The existence of extinction thresholds in metapopulation models, and the concept of the lagged effect of previous losses on persistence, has helped to stimulate interest and focus the minds of ecologists and conservationists. Two important practical messages stand out clearly from the recent literature. Firstly, the non-linear behaviour of the metapopulation dynamics strongly suggests that even if populations have persisted with historical patterns of habitat loss, survival of even trivial amounts of extra fragmentation is not certain. Secondly, the existence of extinction debts suggests that even if populations persist currently, they may still have little future even if further habitat fragmentation does not occur. Both messages indicate that understanding extinction is urgent, as small amounts of extra habitat loss though fragmentation could precipitate an anthropologically driven "mass extinction", if it is not already in progress.

The study of extinction thresholds and associated concepts has been driven by theory. A search of Web of Science using the phrase "extinction threshold" yielded 24 papers over the period 1996–2002, of these the majority are purely theoretical (63%, $n = 15$) in that they investigate extinction in general models, 8 (33%) are more empirically motivated in that they parameterise models with data from single species population studies. The last paper (Eriksson & Kiviniemi 1999) is empirically more general and more experimental, and is based on estimating extinction thresholds based on analyses of site occupancy (survey results) and site suitability (sowing experiments) for 18 species of plants from grasslands in Scandinavia.

This current issue of the journal results from the conference organised by the Spatial Ecology Group of the University of Helsinki, and held in September 2002. The topic of the conference was "Extinction Thresholds: insights from ecology, genetics, epidemiology and behaviour". The majority of contributions to the conference were not about extinction thresholds in the "narrow sense", but were more concerned with processes which may influence extinction, and ranged from theoretical, to experimental, to descriptive. As such, the work presented at the conference allows some insight into the "state of the art" of the ecological study of extinction. Others in this volume will, with greater detail and understanding, review material which is specifically targeted at the topic of "extinction thresholds" (e.g. Bascompte 2003), or material which was covered in specific parts of the conference (e.g. the genetics of extinction — *see* papers by Gaggioti 2003, Jaenike & Taylor 2003, Nunney 2003 and Whitlock *et al.* 2003). Here, I will raise some general issues that arose at the conference, and in so doing, review some of the material which has not found its way into this volume. This is necessarily a somewhat personal account. To add some perspective to this analysis, I also undertook a quantitative review of the literature on extinction. I scanned editions of *Conservation Biology*, *Animal Conservation*, *Biological Conservation*, *Journal of Animal Ecology* and *Journal of Applied Ecology* from 2000 to present (November 2002), and found 261 papers that included the term "extinction" in the abstract or keywords. For each paper, I scored it for:

1. generality of the "question" ("general" or "specific"),
2. generality of the results ("general or specific),
3. whether it was empirically based or theoretical (or a combination),
4. how closely it was related to the study of extinction (on a three point scale),
5. the topic (*see* Table 1), and
6. methodology (*see* Table 1).

Studies of extinction *per se* are rare

Of the 60 or so presentations given at the meeting (approximately 40 talks, *see* Table 2, and 20 posters), there were few that addressed the issues of extinction thresholds directly, and none that really addressed the ecological causes of extinction. Most presentations addressed conservation issues, with many talks investigating the factors that are known or hypothesised to raise extinction risk (for example, population synchrony, small population size, life history etc). As such, the meeting emphasised the prevalence of investigation into the correlates of extinction risk (e.g. what causes population synchrony?), rather than the processes that lead to extinction (e.g. when do populations in synchrony go extinct?). The theoretical presentations on extinction thresholds (e.g. Hanski, Ovaskainen, Frank, Knauer) addressed the issue most directly, as it is possible to do with theory. It is indubitably the case that the empirical study of extinction is difficult (even in well known examples, such as annual patch occupancy in Lepidoptera), not least because it is likely to be highly stochastic. However, this conference suggested that more empirical data on the ecology of extinction would be helpful to guide the future development of theory, and act as a test of existing theory. This conclusion is bourne out by the wider literature (Table 1), where a total of 21 papers (21/244 = 9%) were scored as directly related to studies of extinction (rather than PVAs aimed at management of particular species). The majority of these studies were correlational, based on comparing historical and current presence/absence records with data on habitat change or characteristics.

I coded the information in Table 2 into categories (e.g. by broad subject areas, as per the final column, and coding the other columns according to general *vs.* specific, and theory *vs.* empirical or combination). This allowed some crude analysis which pinpoints the associations found within the table (and, of course, the assumptions and biases I used to construct it). There is a significant association between the "subject" and the specificity/generality of the "answer" ($\chi^2 = 16.2$, d.f. = 4, $p = 0.003$). Not surprisingly, studies looking at population viability tend to lead to conclusions orientated at the study species, compared with studies which look at correlates of extinction risk, which tend to require a cross-species sample. Likewise, studies which tend to pose general questions tend to produce general conclusions ($\chi^2 = 8.7$, d.f. = 1, $p = 0.003$), and general conclusions tend to be associated with theoretical conclusions ($\chi^2 = 14.7$, d.f. = 2, $p = 0.001$). This latter point is worthy of note: much of our general understanding of extinction comes from models, again, suggesting that there is still a need to challenge the models with data to ensure our understanding is solidly, and biologically, based.

In both the conference and the literature searches reported here, there is a strong terrestrial bias. Commercial fisheries provide a fertile field for the study of extinction behaviour, as many fisheries deplete stock to very low levels, including commercial extinction (Enberg & Kaitala 2003). Such exploitation is akin to an experiment and provides opportunities to study demographic changes in response to increased (fishing) mortality, and the interaction between population sizes, environmental processes, and trophic interactions

Table 1. Summary of classification of 261 papers from 5 primary ecology and conservation journals, from 2000–2002. Papers were scored on methodology and primary subject. Eighteen papers were excluded as they were reviews or discussions without methods or data. The subjects were *fragmentation* (including its effects on population size, extinction, dispersal), *extinction* (factors affecting or predicting), *incidence* (presence or absence of organisms in an area, its correlates and determinants), *PVA or MVP* (analysis of a species to determine its viability, or the population size or area needed to make it viable), *single species management* (papers concerning management of a single species, such as range mapping, success of introductions, but not PVA), *population size* (general determinants of population size — other than fragmentation — such as predators, invaders, human populations), *NRD/SAR* (nature reserve design and species area relationships), *priority* (assessing status of species or groups, or the criteria to determine status), *genetics* (conservation genetics, such as inbreeding depression or measures of genetic diversity). The methodology categories were: a) empirical and experimental, b) using a model to conduct experiments, c) descriptive of patterns or process, d) correlative, or e) development of technique or algorithm.

Classification	Empirical experiments	Experiments with models	Descriptive	Correlational	Developing a technique or algorithm	Totals
Fragmentation	5	6	7	13	0	31
Extinction	2	4	0	20	0	26
Incidence	1	0	2	28	0	31
PVA or MVP	0	34	2	6	10	52
Single-species management	1	2	7	6	0	16
Population size	4	7	6	11	0	28
NRD/SAR	1	2	0	6	4	13
Prioritising	0	0	8	6	6	20
Genetics	2	6	12	2	0	22
General theory	3	2	0	0	0	5
Totals	19	63	44	98	20	244

Table 2. Subjective summary of oral presentations at the conference on Extinction Thresholds held in Helsinki in September 2002. The table gives a snapshot of the breadth and focus of studies pertaining to the processes driving extinction. Classifications are subjective, and based on four different criteria: (1) specificity of a topic: is the subject a general one, or is it specific to a particular system, (2) specificity of the answer to a particular system or group, (3) theory or empirically based (including a data-rich model), and (4) broad subject classification. To illustrate the difference between (1) and (2) here are two examples. Firstly, a presentation may be on "fragmentation and extinction risk", which is a very general topic (1), and would be a general (2) if the study made broad conclusions, but would be a specific (2) if the study, and its conclusions were very focused on the single species or system studied. Secondly, a presentation may be on "metapopulation dynamics of species A" would be a specific classification (1) and (2) if the study and its conclusion were oriented towards species A, but would be a general classification (2) if species A were a true model system for a much broader ecological grouping.

Authors	Thumbnail	Specificity of topic	Specificity of answer	Theory	Nature of study
Alroy	correlates of extinction in fossil mammals	general	general	empirical	ecological correlates of extinction
Arlt & Pärt	non-ideal habitat selection	specific	specific	empirical	behavioural correlates of extinction
Armbruster	genetic diversity and breeding system in snails	general	specific	empirical	ecological correlates of genetic diversity
Benton	population synchrony and dispersal	general	general	empirical	population dynamic correlates of extinction
Bergland & Jonsson	extinction debts and forest epiphytes	specific	specific	empirical	extinction debt
Boots	parasite-driven extinction	general	general	theory	extinction and diseases
Bugter	farmland biodiversity	general	specific	empirical	population viability
Cabeza *et al.*	nature reserve design	general	specific	theory/ empirical	population viability
Courchamp & Deredec	thresholds in host and parasite persistence	general	general	theory	extinction and diseases
Fischer & Lienert	fragmentation in *Primula*	specific	general	empirical	ecological correlates of extinction
Flagstad *et al.*	genetic variability in wolves	specific	general	empirical	ecological correlates of genetic diversity
Frank	stochastic extinction thresholds	general	general	theory	extinction thresholds
Garcia-Arenal *et al.*	mutations and persistence of disease	general	specific	empirical	extinction and diseases
Grenfell	metapopulation dynamics of disease	general	general	empirical	extinction, and disease
Griebeler	conservation of *Maculinea*	specific	specific	empirical	population viability
Hanski	extinction thresholds	general	general	theory/ empirical	extinction threshold
Kirkpatrick	geneflow and persistence	general	general	theory/ empirical	genetic correlates of extinction
Kokko & Brooks	sexual selection and persistence	general	general	theory	behavioural correlates of extinction
Knauer	estimating metapopulation survival probabilities	general	general	theory	extinction thresholds
Leimu	population size in *Vincetoxicum*	specific	specific	empirical	ecological correlates of extinction
Loewe	Muller's rachet	general	general	theory	genetic correlates of extinction
Matsinos *et al.*	the ecology of reproductive success in waders	specific	specific	empirical	population viability

Continued

Table 2. Continued.

Authors	Thumbnail	Specificity of topic	Specificity of answer	Theory	Nature of study
Mazaris *et al.*	nesting in Loggerhead turtles	specific	specific	specific	population viability
Mykrä & Vuorisalo	societal attitudes to conservation	general	specific	empirical	determinants of conservation effort
Navarro & Pappinen	Persistence of host-parasite relationship across broad species range	general	specific	empirical	population viability
Ovaskainen	stochastic extinction thresholds	general	general	theory	extinction thresholds
Ranius	metapopulations of *Osmoderma*	specific	specific	empirical	population viability
Reunanen *et al.*	habitat requirements for flying squirrels	specific	specific	empirical	population viability
Revilla	metapopulation dynamics of Lynx	specific	specific	empirical	population viability
Reynolds	life histories and extinction risk	general	general	empirical	life history correlates of extinction
Rintala & Tiainen	decline in Starling populations	specific	specific	empirical	population dynamic correlates of extinction
Ripa & Ranta	population synchrony in trophic systems	general	general	theory	population dynamic correlates of extinction
Séverine	non-random dispersal and colonisation	general	general	theory	behavioural correlates of extinction
Snäll *et al.*	metapopulation dynamics of boreal epiphytes	general	specific	specific	population viability
Travis	climate change and fragmentation	general	general	theory	population dynamic correlates of extinction
Verboom	modelling for management recommendations	general	specific	theory/ empirical	population viability
Vilà *et al.*	genetic rescue and inbreeding in wolves	specific	specific	empirical	genetic correlates of extinction
Vilas *et al.*	inbreeding and genetic erosion in *Silene*	general	specific	empirical	genetic correlates of extinction
Whitlock	Compensatory mutations and threshold population size	general	general	theory/ empirical	genetic correlates of extinction

and so to study the processes of extinction directly as stocks collapse. As such, the very extensive fisheries data may be similar to some of the epidemiological data discussed below: relatively high-quality data, collected for a different purpose, but which may be ecologically illuminating.

Correlates of extinction risk

There are several well recognised correlates of extinction, for example, small population sizes, population synchrony, stochasticity, inbreeding/gene flow and fragmentation. The study of these processes was well represented at the conference (*see* Table 2), but a number of presentations made significant, and general, new inroads in showing the way ahead for understanding some of the processes which drive, or predict, extinction.

John Reynolds showed that there is scope for predicting extinction risk based on characteristics of the life-history, which, in turn, may be predicted using phylogenetic methods. Hanna Kokko, with Rob Brooks, explored the consequences of sexual selection on population viability, with the insight that sexually selected traits are usually considered costly to maintain, implying that a species with exaggerated traits is likely to be in some sense more “at risk” than one without. The converse may also be true, that competition between males may lead to the best individuals passing on their genes, though, in this case, reproductive skew will radically reduce the effective population size (Kelly & Durant 2000). John Alroy explored the correlates of extinction in an extensive database of Cenozoic fossil mammals. Although the analyses tested, and rejected, many predictions, the presentation indicated that amalgamation of ecological data (fossil, or not) into large databases may allow powerful statistical analyses of patterns and processes. Justin Travis pointed out that climate change is now considered an ecological reality, and it is likely to act to degrade the suitability of existing habitat. There is likely therefore to be an interaction between climate change and habitat fragmentation, and as with the issue of extinction debt, purely conserving existing habitat is not likely to be a sure recipe to ensure long-term persistence.

That there is an association between the generality of a study and whether or not it is theoretical (*see* above, Table 2), suggests there is a need to bring more empirical data towards the general theory in order to test it directly, and guide its further development. This challenge of theory with data could come about either through empirical studies that address general questions or through meta-analysis of existing empirical data. An example of the former might be experimental studies, using mesocosms, of the influence of population fragmentation (hence dispersal, colonisation and gene flow) on rates of extinction (e.g. Gonzalez & Chaneton 2002).

The survey of the wider literature indicates a slightly different point. There remains a significant association of theory with general studies ($\chi^2 = 30.4$, d.f. = 2, $p < 0.0001$), but there are also many empirical studies which investigate, and answer, general issues (such as correlating extinction risk and habitat change across taxa). However, what is striking by their absence, are the very few studies of relevant processes in species which are common, and so easy, and ethically possible, to manipulate. For example, Reed and Bryant (2000) conduct an experimental study, using houseflies, to investigate the minimum viable population size, and Gonzalez and Chaneton (2002), experimentally fragment a moss ecosystem and chart changes in population size and extinction. Only 19 (of 244 = 8%) studies involved any experimental manipulation which would allow strong inference about causation, whereas 142 studies (58%) were purely descriptive or correlational. There is surely much scope for such simple, but informative, experiments on non-threatened species to generate information which illuminates processes occurring as populations face extinction in the field.

Collapsing the data in Table 1 by amalgamating the two “experimental” categories, and eliminating the “techniques” category, allows a χ^2 test of association between the subjects and methodologies: $\chi^2 = 120$, d.f. = 16, $p < 0.0005$. This χ^2 largely arises from the association of (1) experimental models and PVA, (2) extinction and incidence being investigated by correlational studies, and (3) genetics and priority-setting (e.g. studies of the form “this species is rare”) being largely descriptive in nature. As outlined above, these associations highlight the methods which are typically not being used, as much as those that are.

Lessons from disease

A hugely important, though not always appreciated, conceptual advance in ecology was made when it was recognised that epidemiology (the study of epidemics, or patterns of diseases more broadly) was an ecological problem (e.g. Anderson & May 1981). The population dynamics of diseases are conceptually similar to the population dynamics of other tropic interactions, like predators and their prey. A pathogen or parasite will go extinct when, in the simplest case, its basic reproductive ratio (the number of infected individuals infected by each infected, R_0) falls below 1.0, its extinction threshold, which, in turn, may occur when the host population falls below a threshold size (the critical community size, as discussed by Franck Courchamp and Anne Deredec). The ecology of extinction can therefore be fruitfully studied by looking at disease persistence, or not. Bryan Grenfell's presentation highlighted that epidemiological data, because they are often extremely extensive and high-quality, may be an important resource for answering more general questions concerning metapopulation dynamics. Mike Boots approached the question of the importance of diseases in population extinction directly and explored the way that sexually transmitted diseases may cause host extinction. He also presented some evidence that diseases may be an important mediator of apparent competition, and so highlighted the risk of invading species displacing the residents because of the differential impact of a shared pathogen.

Genetics

Approximately a quarter of the talks addressed issues associated with the genetics of extinction risk. Mark Kirkpatrick highlighted that geneflow can both have positive and negative consequences for persistence. Gene flow may be negative because it reduces local adaptation, and as such may prevent species occupying its entire available habitat; in contrast, gene flow may have positive effects because it introduces genetic variation into populations, and so counteracts inbreeding and genetic erosion. Mike Whitlock highlighted recent theory on compensatory mutations and how they affect the critical effective population size (below which the population will go extinct through the accumulation of deleterious mutations, via recurrent mutations and drift). Obviously, ecological and genetic processes interact importantly to influence extinction risk, though most presentations given at the conference focussed either on ecological or genetic processes. For example, small population sizes increase the likelihood of inbreeding and genetic erosion (genetic processes), but also make the population more prone to stochastically-driven extinction (an ecological process); together both genetic and ecological processes make extinction more likely than either alone. It would be interesting to more explicitly combine genetic and ecological approaches to extinction. For example, how is the critical effective population size (Whitlock *et al*. 2003) related to the ecological "extinction thresholds"?

Modelling populations in the flesh: case studies and complex models

The conference presented a wealth of "case studies" of the ecology of issues relating to extinction. These ranged from Bryan Grenfell's work on childhood diseases and Foot and Mouth disease, to the metapopulation structure and persistence of *Osmaderma* beetles in ancient, hollow, oak trees, as discussed by Thomas Ranius. Two presentations on the genetics of wolves (by Flagstad *et al*. on reconstructing the history of Scandinavian wolf populations using genetic variability as a measure of gene flow and population size/fragmentation, and Vilà *et al*. on a rare migrational event providing a genetic rescue for an inbred, isolated, wolf population) firmly showed the utility of linking genetics to ecological processes. Markus Fischer and Judit Lienert showed the utility of a careful field study in providing information which informs the ecological correlates of extinction in their particular study species (*Primula farinosa*): isolation led to changes in population size and age structure, changes in susceptibility to smut fungus, changes in predation and a greater proportion of individuals who were on the edge of suitable habitat, and therefore did even more poorly.

A number of studies at the conference had constructed complex models modelling a particular system of interest (*see* Table 2), often to do what amounted to population viability analyses. Once constructed, these models can, of course, be used to study the ecological situations under which extinction can occur. The complexity of some of these models raises an interesting question: how much detail is needed to successfully answer the question that is posed? The importance of the interaction between environmental noise and density-dependence is widely recognised, so one can criticise ecological models without these elements as being too simple, even if the results are qualitatively insightful. On the other hand, can models become too complex? Does there come a point where conservation models become over-parameterised to an extent that they mislead? This could occur, for example, by requiring estimates of many parameters for which precise data are not available. Predicting future population dynamics may become problematical if the models are not properly verified, or if the environment changes, and may lead to over-confidence that the results will be accurate as well as precise. There are a number of studies which show that different models may produce different results (e.g. Gerber & Van Blericom 2001) and that demographic models and historical records may not agree (e.g. Lindborg & Ehrlen 2002), suggesting that over-reliance on a particular model's output is not without risk. There have also been recent calls to ensure that predictions of PVA are accompanied by confidence intervals (e.g. Ellner *et al*. 2002), and that sensitivity analyses of the PVA models be conducted to ascertain the sensitivity of results to parameter uncertainty. An end point of such viability analyses would be to be able to rank the outcomes of different management scenarios (in terms of the expected magnitude of response, as well as the likelihood of its occurrence), which, as pointed out by Jana Verboom, is what managers generally require anyway.

An extinction crisis in human culture?

One of the most stimulating talks was by Bill Sutherland who pointed out that when we think of "extinction" we tend to think about extinction of species and populations, but there is a greater extinction crisis threatening human cultural diversity than is threatening vertebrates. Focussing on human languages as a proxy for culture, he showed that the diversity of different languages was associated with similar factors as is biodiversity (being related to area, latitude, area of forest, altitude etc.). The ecological processes, and tools, that were discussed throughout the conference could therefore be used to inform cultural biodiversity, and study of the change in cultural diversity could be used to inform changes in (organismal) biodiversity.

Summary

The conference, as a scientific meeting, was important for both what was presented and what was not. The cross-fertilisation of ideas that come from mixing epidemiologists, palaeontologists, geneticists, conservationists, theoretical and empirical ecologists, and the different perspectives that come from each discipline was extremely stimulating, encouraging a broader view of both the processes that drive extinction and the tools available to study it. However, it also served to highlight where further work is needed, to make the subject advance as a scientific and predictive subject. The principle area I perceive is the need to join the general theory to data — either through more experimental studies on tractable systems, or by synthesis of the data available from in-depth, species-specific studies. Tractable systems can be used experimentally to obtain understanding of general processes easily. The wealth of data that is available from the largely, single-species-focussed empirical literature of species under threat in the wild, could surely generate understanding through generalisations and synthesis via meta-analysis. In particular, there is a need to understand more the processes that actually caused extinctions. What happens to the individuals, their behaviour, and their survival? The answer given by a population biologist, for example that it is demographic stochasticity, may be unsatisfactory to a behavioural ecologist, who might want individual-level understanding. Although this was a conference entitled "extinction thresholds", the subject of the presentations was much more broadly "the ecology of extinction risk", and, to an extent, highlighted the lack of focus this subject has. By pointing out what is known, what is being done and what is needed, this conference served a valuable purpose and will undoubtedly focus minds, and lead to considerable progress in understanding over the next few years.

Acknowledgements

I thank the organisers, especially Johan Kotze, for the invitation to attend, for the conference organisation, and the invitation to write this overview. This paper benefited considerably from feedback from Mike Boots, Jon Brommer, Hanna Kokko, an anonymous referee and especially John Reynolds and Ilkka Hanski. Finally, and once again, my apologies to the conference centre for breaking their front door as I accidentally, and unsuccessfully, attempted to cross my own extinction threshold.

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