



International Balzan Foundation

Ilkka Hanski

2000 Balzan Prize
for Ecological Sciences

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2000 Balzan Prize for Ecological Sciences

Prize Citation and *Laudatio*

For his outstanding contributions to population and community ecology. His work has profoundly influenced our understanding of how populations in nature persist and how conservation policy for endangered species should be implemented.

Ilkka Hanski is one of the foremost ecologists of his generation. His highly original contributions to both theoretical and observational experimental work in ecological science have had a deep and wide-ranging impact.

More than any other ecologist, Ilkka Hanski has been responsible for the development of the concept of “metapopulations”, one of the most influential ideas in late twentieth century population ecology.

Many species in nature exist as “metapopulations”. A metapopulation is a series of semi-isolated populations linked by occasional migration between them. What Ilkka Hanski has done, building on an idea put forward by Richard Levins, is to show how the persistence of populations often depends critically on the way in which they are divided into sub-groups. Even though any single sub-group may be vulnerable to extinction, the population as a whole persists as a result of movement between sub-groups.

This work is of great importance in conservation. Many endangered species survive in small isolated pockets of suitable habitat.

Ilkka Hanski’s other contributions to ecology are wide-ranging. For example, he has done exquisite work on the structuring of ecological communities and made important contributions to our understanding of the well-known population cycles of voles and lemmings. Ilkka Hanski’s world-wide influence has come from the many papers he has published, his books, and from the students he has supervised.

Prizewinner's Acceptance Speech

Rome, Accademia Nazionale dei Lincei, 15 November 2000

*Mr. President,
Members of the Balzan Foundation,
Ladies and Gentlemen,*

I have the greatest pleasure, and the tremendous honour, of representing here the large community of ecologists as the recipient of the Balzan Prize for Ecological Sciences. With this prestigious prize I feel like the smallest in a set of Russian dolls, surrounded by multiple layers of science and scientists. Today I wish briefly to describe to you some of the bigger dolls in this set. But before doing that, allow me to express my appreciation and praise for the two recent subjects chosen by the International Balzan Foundation in the field of biology to receive this prize, biodiversity in 1998 and ecological sciences today.

Though as an ecologist I can hardly be expected to be impartial in this matter, I think we all agree that the broader aims of the Balzan Foundation, to advance culture and science, and peace among people, are difficult to achieve in the long term unless our human race finds harmony with the other creatures, with which we share not only common ancestry but also this planet.

One of the Russian dolls inside which I reside is a relatively new approach in population ecology, dubbed spatial ecology, which I, along with many others, have pursued over the past 20 years. Spatial ecology is based on the general notion that the spatial locations of individuals in their habitat, and the ensuing spatial structure of populations, can have as profound consequences for population dynamics and for the biology of species in general as the more familiar ecological processes, such as birth and mortality rates, competition and predatory skills. 1998 Balzan Laureate, Sir Robert May's outstanding contributions towards unravelling universal patterns in biological diversity have been duly recognised. Many of these patterns are greatly influenced by the spatial structure of the environment and of populations. To give an example, the astonishing diversity of insect species, estimated at around 4 million, may have much to do with the small-scale heterogeneous spatial structure of their populations, which is generally expected to facilitate the coexistence of species. With such distinctive creatures as dung beetles and carrion flies as my assistants, I have aspired

to develop and test models about the role of spatial structure in the ecology of populations and communities.

In the past 10 years, my research has been largely focused on metapopulation ecology, which represents one particular kind of spatial ecology. In the 1970s, the dynamic theory of island biogeography, established by Robert MacArthur and Edward Wilson, emerged as a bright beacon, guiding the research of hundreds of population and community ecologists world-wide and providing a much-needed conceptual framework for conservation biology. This theory was originally developed to understand patterns of biogeography on islands and archipelagos, but it was soon applied to island-like situations on land – such as nature reserves in human-modified landscapes. One sign of the enormous speed of contemporary environmental change is that the new (though related) vision, metapopulation ecology, is now replacing the theory of island biogeography in conservation. With this shift in the theories, emphasis has moved to smaller spatial scales, to ordinary fragmented landscapes. Rather than ask questions about particular fragments of landscape, we now ask questions about the properties of entire networks of habitat fragments, and how these properties will influence the ability of species to persist, maintenance of genetic diversity, and the capacity of species to evolve in a changing environment. To avoid any misunderstanding, this change in the theories by no means implies that large reserves are now of reduced value in terms of conservation. Paradoxically, the opposite is the case, but it is natural for ecologists to become concerned with fragmented populations in our increasingly fragmented world.

Population ecologists include hard-core theoreticians as well as devoted empiricists. Having been attracted to both camps I have, as a result, stayed in the middle ground. Ecological phenomena are complex, which both necessitates an effective combination of theory and empirical research, but which also makes it hard to achieve that combination. I have had the very good fortune of working together with researchers having dissimilar talents, and I believe that through these collaborations we have been able to make many of our best contributions.

I am particularly overwhelmed by this recognition, both as a citizen of a small nation and as a scientist in the middle of his career. I understand that with this prize the Balzan Foundation intends to acknowledge the relative strength of ecology in Finland and in many other small countries. Ecology is indeed a field of science where important contributions of all kinds have been made by researchers working outside the big centres of scientific discovery. I accept this prize as a challenge for myself and for ecologists in Finland and other small na-

tions to continue to work with the aim of making truly significant contributions to our science.

The largest doll in my set is the changing position in which we ecologists find ourselves. Natural habitats are being lost and fragmented all over the world at a distressing rate. The human causes of climate change are becoming increasingly evident. As human beings we may experience globalisation and an expanding world – for most other species on earth though, the world is rapidly shrinking. Habitat fragmentation compounded with climate change poses a massive menace to species. Whether we like it or not, the mission of ecology will increasingly be linked with the entirely justified concerns about the state of our environment and about the future of biological diversity.

As scientists, we have to maintain and increase the standards of our work, including the need to assess facts as objectively as possible. At the same time we cannot hide away from the responsibility of speaking out about the likely consequences of the current course of human expansion.

I am deeply grateful for the magnificent recognition that I have received today. By assigning this prize to the ecological sciences the Balzan Foundation has greatly increased the general respect for ecology.

Ilkka Hanski

A Panoramic Synthesis

by Ilkka Hanski

A panoramic synthesis of his career,
realized on the occasion of the 2000 Awards Ceremony

INTRODUCTION

I was 11 years old when an event occurred to which I can trace my teenage wish to become a biologist. The date was August 18, 1964. I had the childhood luxury of spending all my summers in the countryside, where, following the example of some older boys, I had taken up collecting insects. On that day I caught a brown butterfly that I could not name using my small handbook. Looking through a more advanced work which my parents had bought me in the autumn, I found that my mystery insect was a female of *Hyponephele lycaon*, a species that had not been recorded in Finland since 1936. My observation was communicated to Professor Esko Suomalainen, a geneticist well known for his pioneering work on parthenogenesis, who had published a paper on the declining populations and eventual extinction of *Hyponephele lycaon* in Finland (Suomalainen 1958). My amazement was great when, a few days later, I found in the mail a copy of Suomalainen's paper, which I could not read as it was written in German, but which became an instant treasure to me as a small boy.

By a curious coincidence, 35 years later my own research had turned to the very questions explored by Suomalainen in his paper. *Hyponephele lycaon* was the first species of butterfly to become extinct in Finland in historic times, possibly because of a temporary cooling in the climate which may have been responsible for a decline in the extent of suitable habitat for this species. (The female that I had found in 1964 was probably a vagrant from outside Finland). Suomalainen was particularly interested in the possibility that the final demise of *Hyponephele lycaon* was due to harmful effects of inbreeding in the small dwindling populations in the 1930s. The coincidence is that, working on the second species of butterfly to go extinct from mainland Finland (*Melitaea cinxia*), we have now produced the first conclusive evidence of its kind that

inbreeding indeed increases the risk of extinction of small natural populations (Saccheri et al. 1998, Nieminen et al. 2001).

I entered the University of Helsinki to study Zoology in 1972. As a first-year student, I initially felt destined to a career in a museum, studying entomology, but I soon realised that there was nothing to prevent me from becoming an ecologist instead of a systematist – and an ecologist I became. No doubt my mind was changed by the atmosphere of great excitement in ecology in the early 1970s, and though I was a student in Finland, outside the big centres of scientific discovery, current trends were eagerly assimilated. It was not just a single new direction that ecologists were exploring in those days; several new approaches were established and developed, from behavioural and evolutionary ecology to mathematical population and community ecology to ecosystem ecology. I was living in the midst of keen peers but had only foreign heroes; the transition from old field biology to modern ecology was rather abrupt in Finland.

I became associated with an ecological entomologist, Hannu Koskela, who was engaged in a study of the beetle community living in a habitat that only small boys and ecologists love to inspect, cattle dung in pastures. A fascinating community with dozens of species coexisting in the same place and apparently using the same resources! This was a challenge to community theory, and we joined forces to examine the niche relations in this assemblage of ‘too many’ beetles in a limited space (Hanski and Koskela 1977). I became excited by the opportunities for research with insect communities living in cattle dung and in animal carcasses. My first piece of field work was based on the idea of experimentally transferring the entire community of carrion-feeding insects from one ‘macrohabitat’ (forest) to another habitat (field), and vice versa, to investigate the causes of obvious differences in the species composition in the respective communities. In another experiment I manipulated the environmental conditions for the carrion fly community by raising the ambient temperature with a heating cable buried in the soil below the experimental carcasses. These experiments were moderately successful, and they taught me that an ecologist with some imagination could do interesting things without expensive facilities. In 1976, the opportunity arose for me to see one of the big centres of scientific discovery, Oxford University, where I did my DPhil, continuing with my studies on insect communities but also developing a lasting interest in spatial population structures and dynamics.

INSECT COMMUNITIES AND SPATIAL POPULATION STRUCTURES

In his Balzan article on biodiversity, Sir Robert May (1999) put the species richness of insects on Earth at 4 million species, of which less than a quarter have been scientifically described. Local species richness, which is what community ecologists are supposed to be able to deal with, is measured in thousands of species. For anyone fascinated by the sight of very many species in a very small space I can give no better advice than to go and look at the insect life in cattle dung. At the same time, this community highlights the problems of unveiling the dynamics of ecological '*n*-body problems', with thousands of direct and indirect interactions between pairs of species.

Some broad issues may not be hopelessly intractable, however. The question regarding the coexistence of large numbers of similar species in the same community is one such general issue. I spent weeks and weeks pondering this question in the late 1970s, without realising that valuable advice might have been obtained locally. Charles Elton, one of the greatest names in the history of ecology, had retired in Oxford in 1967, following a bitter and unsuccessful fight to keep his Bureau of Animal Population alive after his retirement. In the late 1970s, Elton used to come to his office once a week, which gave me the chance to talk to him on several occasions. Regrettably, I had not read his presidential address to the British Ecological Society, published in 1949. In this paper, Elton was decades ahead of his time when he complained about ecological theories being based upon notions of mean density. In his words, ecologists «must learn to take account of the fact that populations are split up into groups or centres of action...». In 1981, Atkinson and Shorrocks (1981) and I (Hanski 1981), working independently on fruit flies and dung beetles, respectively, showed with simple models how right Elton was. The idea is quite straightforward. If species have spatially aggregated distributions, most individuals occur in high-density patches, Elton's centres of action, whose situation necessarily increases the level of competition experienced by an average individual in the population. Secondly, if different species are aggregated at least to some extent independently of each other, spatial aggregation will intensify intraspecific competition more than interspecific competition, and hence spatial aggregation will facilitate coexistence. The point is that, as Elton had observed, spatial aggregation is ubiquitous in real populations, and different species practically never show completely correlated spatial distributions. Here, therefore, is a mechanism that very generally makes it easier for many species to coexist. In my contributions, I combined theory and

simple models with observational and experimental field work, which produced conclusive results (Hanski 1990). It gave me much satisfaction to demonstrate for myself and to others how the aggregation mechanism worked both in theory and in real communities.

The line of research described above clarified the population dynamic consequences of spatial aggregation, but it left largely open the question about the causes of the observed population aggregation, in other words the dynamics of spatial aggregation itself. In the case of insect populations, this is a hard problem, because population aggregation is here largely due to interaction between complex structure of the habitat and complex behaviour of individuals. Much later, in the 1990s, ecologists focusing on more tractable systems, plant communities inhabiting relatively uniform habitats, have made great progress in modelling both the consequences as well as the population dynamic causes of spatial population structure (Bolker and Pacala 1997, Law and Dieckmann 2000). One of the challenges that remains is to incorporate in the models heterogeneous habitat structure.

What I have written above about spatial population structures and their population dynamic consequences applies to small-scale spatial structure, observed at the scale of single local populations. In 1959, Professor L.R. Taylor working at the Rothamsted Experimental Station initiated an ambitious long-term project to investigate simultaneous changes in time and space of population size in more than 800 species of moths and aphids. Over one hundred sampling stations were established across the UK, which produced, in the due course of time, an unparalleled picture of large-scale spatial dynamics in insect populations (the 'Rothamsted survey' is still going on, and the concept has been imported to several other European countries). Working together with Ian Woiwod and Joe Perry from Rothamsted, I was able to clarify several key questions about population dynamics using the results of the Rothamsted survey. These data conclusively demonstrate regulation even of the populations of insects that appear to oscillate wildly (Woiwod and Hanski 1992), they show how changes in population size are spatially autocorrelated at a large scale, most likely because of similarly correlated environmental conditions (Hanski and Woiwod 1994a), and new insight was gained into the structure of stochasticity in insect population dynamics (Hanski and Woiwod 1994b). Another unique population data set which I have had a chance to work with describes the multiannual population oscillations of small rodents in Fennoscandia, which exhibit one of the best-described cases of complex dynamics in animal populations (Hanski et

al. 1993, Hanski and Henttonen 2001). In the 1980s, there was a period when observational studies were not highly valued in population and community ecology, the focus having shifted to experiments. Today, luckily, a more balanced view prevails, and we realise that there is no substitute for long-term spatially extended data series in ecology, which both tell us what we need to explain and which provide the bench-test against which to assess our theories.

THE METAPOPOPULATION PERSPECTIVE

One of the truly novel ideas that was introduced in ecology in the late 1960s is the dynamic theory of island biogeography (MacArthur and Wilson 1963, 1967). Originally developed to explain the dynamics and the pattern of occurrence of species on islands with dissimilar areas and distances from the mainland, the 'island theory' soon captivated the minds of ecologists at large and was widely adopted by conservation biologists. In a nutshell, the theory explained the distribution of species on islands in terms of area-dependent extinction and isolation-dependent colonization; the number of species to be found in any particular island, or in a nature reserve, would represent, according to this theory, the outcome of the opposing forces of extinction and colonization.

In the late 1980s and early 1990s the island theory began to give way to a new perspective, and a new set of theories, based on the concept of a metapopulation. The metapopulation concept had originally been developed by Richard Levins (1969) at the time when MacArthur and Wilson were working on their island theory, in the late 1960s, but curiously the idea remained dormant for some 15 years. It is also one of the mysteries in the history of population ecology why MacArthur and Levins, who knew each other well, did not produce straightaway a more general theory that would have encompassed their respective models as special cases. The essential difference between the two conceptual frameworks is that the island theory includes a mainland, a permanent source of colonists, whereas the Levins model is concerned with the dynamics of species in networks of habitat fragments without a mainland, and hence a species may become permanently extinct in the Levins model. The island model was specifically focused on the effects of island area and isolation on extinction and colonization, whilst the original Levins model assumes an infinite number of identical habitat fragments. My own contribution in the 1990s was to produce a synthesis of the two models, allowing for spatial variation in habitat fragment areas and

connectivities in finite patch networks without a mainland (Hanski 1998, 1999). We now have a relatively well-developed theory (Ovaskainen and Hanski 2001) and models that can be parameterized with empirical data (Moilanen 1999) and applied to real metapopulations to generate quantitative predictions about the distribution of species in highly fragmented landscapes (Wahlberg et al. 1996, Moilanen et al. 1998). We can answer questions about the capacity of fragmented landscapes to support viable metapopulations of particular species (Hanski and Ovaskainen 2000), and though the models do not yet incorporate all relevant processes, such as regional stochasticity, they will soon do so. My hope is that the kind of ‘spatial realism’ that the current ecological models of metapopulation dynamics incorporate would next be transported to genetic and evolutionary models.

The major shortcoming of the metapopulation theory that I have helped construct is that it applies primarily to ‘highly fragmented’ landscapes, by which I mean landscapes in which the habitat of interest occurs as a network of discrete fragments. It remains a big challenge to develop comparable theories for landscapes with a less well-defined structure. On the other hand, another line of theoretical research on spatial dynamics assumes no landscape structure at all (Hanski 1998), these theories being concerned with the conditions under which population dynamic processes alone may generate and maintain spatial variation in population density. One of the challenges for research in this area of ecology is to produce a more unified theory that would incorporate in one framework the different approaches that we now have, to spatial population dynamics.

THE SHRINKING WORLD

Several factors have contributed to the shift from the island theory to metapopulation theories (Hanski and Simberloff 1997), of which one no doubt is the ongoing worldwide transformation of natural landscapes. With real landscapes losing ‘mainlands’, large continuous areas of natural habitat, the metaphor of islands located outside a large mainland is becoming a poor metaphor. While we humans with a few other species experience globalisation, for most species the Earth is shrinking and breaking up into small, disconnected pieces. It is inevitable that increasing numbers of species will become extinct, not just hundreds of species but thousands, tens of thousands and hundreds of thousands of species.

Perhaps a few million species will become extinct in the coming decades and centuries, of the order of half of the current stock of species.

During my first year at Oxford, I had the honour of having Charles Elton, already an old man, attending my seminar. I talked about the community of dung beetles and about the problem of coexistence of great numbers of species in spite of seemingly limited differences in their ecologies. Elton asked me which species I considered as most important in the community. I could not name such species, an answer that appeared to please him. Nor should we attempt to name, today, the species that are important enough to be allowed to survive. This question is not about science, of course, but there is no reason why scientists should not express their anxiety about short-term human greediness permanently eradicating much of the natural beauty in the world as well as parts of the living machinery tested by billion-year-old evolution. As we should know, our own existence is ultimately dependent on this machinery.

Depressing as it is, there is little hope that the present trajectories of global change will take a sudden turn. In the case of habitat loss and fragmentation, the task of population ecologists is to gain better understanding of the biological consequences – and to make sure that this understanding is conveyed as accurately as possible to society at large. Apart from that, one can only hope that, at some point in the foreseeable future, this society will be ready for action to slow down and ultimately to stop and reverse the current trends of environmental deterioration.

THOUGHTS ON POPULATION ECOLOGY

I have suggested that the current popularity of metapopulation theories is partly due to the obvious need to better understand the population consequences of habitat loss and fragmentation. It is also important that the current models have been successful in giving guidance to empiricists in the planning of their research. In a similar manner, the island theory of MacArthur and Wilson became so popular so quickly in its time largely because it gave a simple explanation to a universal pattern in the distribution of species, the species-area relationship, and made empirical research on this pattern so much more interesting. In both cases, a key component is the mapping of the population dynamic processes of extinction and colonization onto the structure of the landscape, described in terms of the areas and connectivities of islands, reserves or any other fragments

of habitat. That such area and isolation effects occur is almost a truism, given basic understanding of population dynamics and dispersal, but the challenge is to produce a theory that will explain these effects in quantitative terms.

Much of theoretical ecology suffers from a lack of meaningful bridges to empirically-based research. Combining theory and research on real populations is difficult in ecology, because ecological systems are characterized both by historical contingency (populations and communities are perturbed by processes operating at many scales) and great dynamic complexity (many species with innumerable direct and indirect interactions). Frustrated by the failures to develop a predictive theory at the scale of individual communities, some ecologists have advocated an approach dubbed macroecology. Macroecology is focused on large-scale statistical patterns in the distribution and abundance of species and in measures of community structure, such as the distribution of body sizes. Unfortunately, documenting these patterns at large spatial scales may not increase our understanding of the relevant ecological processes. In this respect, I consider that the area and isolation effects on extinction and colonization, which are the cornerstones of much of the current metapopulation theory, represent 'macroecology' at a proper scale, not too small to require the hugely difficult reductionist analysis of local populations and communities, but small enough to retain a handle on the relevant processes.

One approach to strengthening the dialogue between theory and empirical research in population ecology is via large-scale projects that employ a particular population, metapopulation or a community as an 'ecological research facility' to address broad issues. In such a context, one may accumulate a sufficient body of information and knowledge to deal with the problems of historical contingency and complex interactions, and one is in general in a good position to promote a balanced advancement of theory and empirical research. In my research group, we have focused on one such ecological research facility for the past 10 years, a large metapopulation of the Glanville fritillary butterfly (*Melitaea cinxia*) in the Åland Islands in the northern Baltic (Hanski 1999, chapters 11 and 12). The backbone of this research is a data base on thousands of habitat fragments suitable for the species, supplemented with a range of remote-sensed information to describe the environment. We monitor all local populations, which number several hundreds in each year, and we have gradually accumulated knowledge of more than 1000 population turnover events, extinction and colonization. It is clear that developing predictive models is greatly facilitated by such a mass of knowledge and information, and it is simply very helpful for

the more narrowly-defined research projects of students and researchers to have that knowledge available as a context into which to place their own results. Many other ecological research projects are even bigger than ours, but it is probably fair to say that the great bulk of population ecological research continues to be conducted without the benefit of knowing the ecological context. Much potentially useful information will be lost because of fragmentation of our pooled research effort. The community of ecologists must learn to define its research priorities and to find the means of implementing the research at a scale that is required to advance our science (Lawton 2000).

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Biographical and bibliographical data

Ilkka HANSKI, born in Finland, on 14 February 1953, is a Finnish citizen. MSc (1976) at the University of Helsinki and DPhil (1979) at Oxford University. Professor of Zoology (Animal Ecology) (since 1993) at the University of Helsinki, and Research Professor of the Academy of Finland (since 1996).

Director of the Metapopulation Research Group, which has been chosen as a centre-of-excellence in research by the Academy of Finland for the periods 2000-2005, 2006-2011 and 2012-2016.

He has taken part in and continues to contribute to the work of the international scientific community, being a member of scientific councils, institutes and overseas societies, and two panels of the European Research Council.

He has served as the associate editor or member of the editorial board of numerous international journals.

Academic honours and awards

- 2011 The Kempe Award for Distinguished Ecologists, Umeå, Sweden
- 2011 Honorary Fellowship of the Queens's College, Oxford
- 2011 Crafoord Prize in Biosciences
- 2010 European Latsis Prize 2010 for biodiversity
- 2010 The Environment Award of the Finnish Association for Nature Conservation
- 2010 Foreign Associate of the National Academy of Sciences, US
- 2010 Honorary doctorate, Norwegian University of Science and Technology
- 2008 Lauri Jäntti Foundation's Nonfiction Literature Prize for the book *Viestejä Saarilta*
- 2007 Finnish Science Award
- 2007 E.J. Nyström Prize of the Finnish Society of Sciences and Letters
- 2007 Finnish State Prize for dissemination of information
- 2007 Corresponding Fellow of the Royal Society of Edinburgh
- 2006 Member of the Finnish Society of Sciences and Letters
- 2006 Honorary Foreign Member of the American Academy of Arts and Sciences
- 2005 Foreign Member of the Royal Society of London
- 2005 Marsh Award for Ecology, the British Ecological Society
- 2005 Science Award of the City of Helsinki

- 2003 Honorary professorship in the Peking Normal University, China
- 2002 Foreign Member of the Deutsche Akademie der Naturforscher Leopoldina
- 2002 Suomen Valkoisen Ruusun I luokan ritarimerkki (Finnish decoration)
- 2001 Member of the Finnish Academy of Science and Letters
- 2001 The Sewall Wright Award of the American Society of Naturalists
- 2000 Foreign Member of the Royal Swedish Academy of Sciences
- 2000 Balzan Prize for Ecological Sciences
- 1999 International Ecology Institute (ECI) Prize in Terrestrial Ecology
- 1999 President's Gold Medal, the British Ecological Society
- 1998 Member of the Academia Europaea

Books and edited volumes

- *Viestejä saarilta. Miksi luonnon monimuotoisuus hupenee?* (book in Finnish about biodiversity), Gaudeamus, Helsinki, 2007;
- *The Shrinking World: Ecological Consequences of Habitat Loss*, International Ecology Institute, Oldendorf, 2005 (translated into Russian, Chinese and Finnish);
- *Ecology, Genetics, and Evolution of Metapopulations*, edited by I. Hanski and O. Gaggiotti, Elsevier, Academic Press, Amsterdam, 2004;
- *On the Wings of Checkerspots: A Model System for Population Biology*, edited by I. Hanski and P.R. Ehrlich, Oxford University Press, Oxford, 2004;
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