Patchy diversity –
How do animal and plant populations survive in fragmented habitats?

*The 2011 Crafoord Prize in Biosciences has been awarded to the Finnish ecologist **Ilkka Hanski** of the University of Helsinki. His innovative research on metapopulation ecology has greatly enhanced our awareness of how plant and animal species are affected by growing habitat fragmentation due, for example, to deforestation, urbanisation and climate change.*

The United Nations International Year of Biodiversity has just ended. More and more people have come to understand that biodiversity is under threat, and that it is vital to human well-being. In October, the nations that signed the Convention on Biological Diversity met in the Japanese city of Nagoya and agreed on a new global vision to halt biodiversity loss by 2020. Key proposed measures in the package include protecting 17% of the world's land and inland water areas, and 10% of marine and coastal areas, from exploitation. But is this really enough? Answering this question calls for extensive knowledge of how plant and animal species are dispersed in landscapes, and how they are affected by the ongoing fragmentation of habitats caused by, for example, deforestation, urbanisation and climate change.

This is the context in which the Laureate of this year's Crafoord Prize in Biosciences, the Finnish ecologist Ilkka Hanski, has conducted his pioneering research. In a scientific career of more than 30 years, he has carried out extensive field studies. He has also developed new analytical methods and mathematical models that have contributed substantially to the development of population biology as a whole. The pivotal feature of Hanski's research is his theories on the dynamics of *metapopulations*, in which he proposes ways of solving crucial problems associated with the conservation and sustainable use of biodiversity in increasingly fragmented landscapes.

At the outset of his research career, Ilkka Hanski focused mainly on the composition and interrelationships of various insect populations in small-scale, fragmented habitats. Since then, his research has gradually become more oriented towards regional connections, including genetic and evolutionary implications at landscape level. Today, Hanski's models are standard for studying endangered species, since one of the greatest threats they face is this very fragmentation of landscapes. His research on butterflies, dung beetles, voles, lemmings, water fleas and other organisms has propelled the development of a new field, *metapopulation ecology*, that is now one of the cornerstones of biodiversity conservation and of our scope for predicting how animal and plant species may be affected by, for example, land use and climate change.

METAPOPULATIONS

In ecology, the term *population* is used to describe all individuals of a particular animal or plant species that inhabit a defined geographical area over a long period. A *metapopulation* is a network of local populations in which these populations are partially isolated from one another, but some flow of individuals and exchange of genes among them nonetheless takes place. Not all species occur in metapopulations but in the fragmented landscapes of today, suffering ever greater human impact, a substantial and rising number of plant and animal species are patchily dispersed in the landscape and function like metapopulations. See also figure 1.

From population to metapopulation

Different populations of a particular species are thus relatively discrete groups, among which limited exchange of individuals and genes takes place. Thus, for example, all the people in Sweden or all the Great Tits on the island of Gotland are known as a "population". How many individuals a population contains (its *abundance* or density) is, as a rule, determined by four basic figures: the numbers being born (nativity), dying (mortality), moving into (immigration) and moving out of the area (emigration). A *metapopulation*, in turn, is a "superpopulation" comprising two or more subpopulations, patchily dispersed in the landscape. Its preservation depends on the subpopulations' risk of extinction and on their recolonisation.

The term "metapopulation" was coined by Richard Levins back in 1970. But it was not until Ilkka Hanski conducted his large-scale field studies and devised his innovative models that metapopulation theory became generally accepted among ecologists.

Analysing metapopulations has enabled Hanski and his research team, the Metapopulation Research Group (MRG), to elucidate the critical degree of habitat splitting, when the long-term survival of a given species can no longer be expected. Their research has thus contributed important new knowledge on how and why species die out, but also new insights into how endangered species can nonetheless survive in a fragmented environment.

From Sarawak's rainforests to Åland's dry meadows

In a career spanning more than three decades, Ilkka Hanski has been on expeditions to such exotic places as the unique Sarawak rainforests of Borneo and the distinctive, biodiverse natural environment of Madagascar. He has carried out research as far afield as China and Greenland. But it is in fact in Finnish territory, among the butterflies in dry meadows on the Åland islands in the Baltic Sea that Hanski has carried out his most acclaimed studies, which have established him as one of the world's most eminent ecologists.

Butterflies as model organisms

Hanski and the MRG have devoted more than 20 years' research to a specific butterfly species: the Glanville Fritillary (*Melitaea cinxia*). Their well-planned, extensive field studies of the butterfly populations on the Åland islands are classic among research ecologists who investigate how species are affected when their habitats undergo splitting. The Glanville Fritillary is a butterfly with a wingspan of 30–40 mm, covered with a beautiful checkerspot pattern of brownish-black and brownish-yellow (figure 2). Its range is the whole of Europe, North Africa and, to the east, from Russia to the Middle East. In Northern Europe, however, the numbers have declined and the range has become fragmented over the past few decades as modern agriculture has transformed the landscape. The species is no longer found on the Finnish mainland, but survives in split metapopulations on the Åland islands in the Baltic Sea (figure 2), where Ribwort Plantain (*Plantago lanceolata*) and Spiked Speedwell (*Veronica spicata*) are the key host plants for the larvae of this butterfly species.

Hanski and the MRG's fascination with this exquisite little butterfly has not just been a matter of learning all about the biology of an individual lepidopteran. This specific species was chosen for modelling purposes in order to develop a generally applicable theory of how animal populations are affected by habitat fragmentation due to changes in the landscape. The Glanville Fritillary remains Ilkka Hanski's foremost object of research.

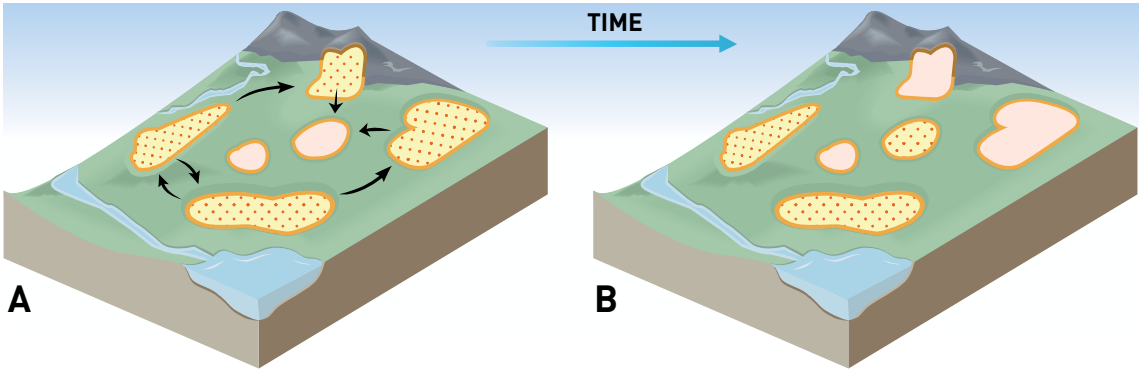
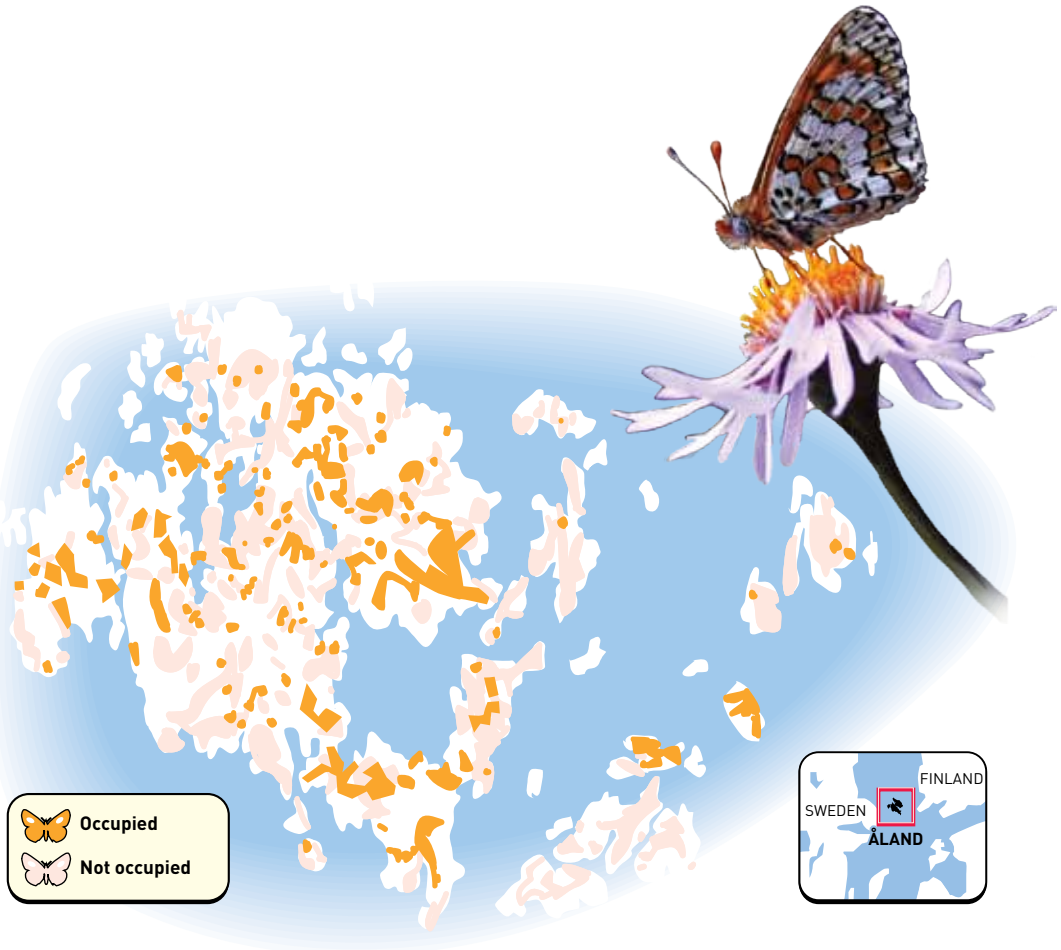


Illustration: Jimmy Blomqvist/©The Royal Swedish Academy of Sciences

Figure 1. A metapopulation of a particular plant or animal species consists of a network of several populations that are patchily dispersed among various places or *habitats* (**A**) in the landscape. The local populations are partially isolated from one another, but some flow of individuals and exchange of genes nonetheless take place. In the range of such a metapopulation, at any given time, only a certain proportion of the suitable habitats are *occupied* (dotted areas), while others are *unoccupied* (light-coloured areas). Movements take place among the various habitats (as shown by the arrows in the diagram) and may result in suitable new areas being colonised by the species. At the same time, there is a risk of certain local populations becoming entirely extinct. After a while, the distribution of the metapopulation in the landscape has therefore changed (**B**). Thus the two processes of local populations, *colonisation* and *extinction*, give rise to *the metapopulation's dynamics*.



Butterfly photograph: Niclas Fritzén
Illustration: Jimmy Blomqvist/©The Royal Swedish Academy of Sciences

Figure 2. Map showing the range of the Glanville Fritillary (*Melitaea cinxia*) in the Åland islands. The dark patches represent areas where this butterfly species is found, while the light ones show habitats that are suitable for the species but nevertheless uninhabited. Ilkka Hanski's research team has been surveying these split habitats in the Åland islands annually since 1993. This long time series has yielded an extensive understanding of metapopulation ecology and important new knowledge of how survival of plant and animal species can be achieved in an increasingly fragmented landscape.

Dung beetles too

Ilkka Hanski embarked on his research at Oxford University, where he took his PhD in 1979 after a detailed pioneering study of dung-beetle ecology in Madagascar. Since then, he has also studied dung beetles in Finland, on the Indonesian island of Sulawesi and elsewhere. Dung beetles live in and on the droppings of herbivorous animals, and play a highly significant part in the breakdown of organic matter in the natural environment. Hanski is still engaged in a research project in Madagascar, focusing on the 300 unique species of dung beetle that are endemic (found nowhere else in the world). These ecologically important decomposers have, in Hanski's research, proved to be of outstanding interest as objects of research when it comes to understanding the workings of metapopulations, not least because they are extremely vulnerable to habitat loss and modified land use. This research has been so highly appreciated that Hanski has had two species of dung beetle named after him: *Onthophagus hanskii* and *Phacosoma hanskii*.

Major bearing on nature conservation

Ilkka Hanski's metapopulation research on animals from butterflies and dung beetles to lemmings and brown bears, has also made the term *extinction debt* generally known. It means that species may live on in fragmented, isolated populations despite being doomed to disappear in time, owing to the great changes in their habitats that have already taken place. The butterflies Hanski himself has studied have, for example, proved to have been weakened by inbreeding and deterioration in flying ability when splitting of subpopulations has gone too far, impairing the metapopulations' long-term survival potential and capacity to withstand environmental changes. Similar patterns have been observed for many other species in landscapes that have progressively disintegrated with the expansion of human land use.

In this way, Ilkka Hanski's research has a major bearing on practical nature conservation and biodiversity policy, since the phenomenon of extinction debt can lull us into a false sense of security, i.e. make us believe that biodiversity is stable in an environment where many species are, in fact, condemned to die out in the long term. A common misconception in this context is that small deteriorations in the habitat are always followed by a linear, and thus predictable, decline in biodiversity. Hanski's butterfly research shows, on the contrary, that the connection is by no means linear: rather, populations often collapse entirely when a particular critical point or threshold is reached and habitat splitting has gone too far.

Once a collapse of this kind has taken place it may be difficult, not to say impossible, to reverse the trend and save the endangered species. One requirement might, for example, be more environmentally sound forestry that saves individual trees in the hope that some insect or bird population under duress will recover. But no recovery will take place, according to Hanski's research, if the population remains below the critical limit. His findings indicate that a large number of species are condemned to die out in Finland alone, even if not one more tree is felled. One implication of this type of knowledge is that it is usually better to be proactive in nature conservation than to wait and risk having to take costly, difficult measures to assist endangered species only when a majority of their populations have already collapsed.

Active in social debate

Ilkka Hanski's great scientific breadth has had an impact, as mentioned above, beyond metapopulation ecology itself – for those engaged in practical nature conservation, for example. Hanski is also the kind of researcher who likes to make a personal contribution to popularising and disseminating his own research findings. In interviews, he has emphasised that the ecologist community bears a responsibility beyond that of pure science and should work to make the public and decision-makers alike more aware of the true challenges of preserving biodiversity.

Topics of debates in which Hanski himself has become involved include forest conservation in Finland, Sweden and Madagascar. In his view, for example, the proportion of protected forest in Southern Finland would need to be enlarged at least five times if requirements for forest protection were based on ecological considerations and on his own metapopulation models.

LINKS AND FURTHER READING

More information about this year's prize is available on the Royal Swedish Academy of Sciences' website, *http://www.kva.se/crafoordprize* and at *www.crafoordprize.se*

Popular-scientific article

Butterfly effects, article by Päivi Lehtinen in *Helsinki University Bulletin* 1/2008: *www.helsinki.fi/hub/articles/?article=2*

Book

Hanski, I. (1999): *Metapopulation Ecology.* Oxford University Press, New York, 313 pp.

Scientific articles

Hanski, I. (1998) Metapopulation dynamics. *Nature* 396: 41–49.

Hanski, I., Kuussaari, M. och Nieminen, M. (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology* 75(3): 747–762.

Hanski, I. och Gilpin, M. (1991): Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42(1–2): 3–16.

Websites

CV and publication list: *www.helsinki.fi/science/metapop/People/Ilkka.htm*

More about Hanski's research and the Metapopulation Research Group: *www.helsinki.fi/science/metapop*

THE LAUREATE

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Finnish citizen. Born in 1953 in Lempäälä, Finland. PhD in Zoology from Oxford University (1979). His positions have included Acting Professor of Zoology (Animal Ecology) and Professor of Zoology (Animal Ecology) at the University of Helsinki (in 1988–91 and since 1993 respectively), and Research Professor at the Academy of Finland (National Research Council) since 1996.

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