Ilkka Hanski

(1953–2016)

Population ecologist who modelled how species cope with habitat loss.

Ecologist Ilkka Hanski's pioneering work changed our understanding of how biodiversity is maintained. Combining mathematical modelling and long-term data from the wild, he developed metapopulation theory. This predicts the degree of habitat fragmentation beyond which a species will go extinct.

Hanski's 1999 book *Metapopulation Ecology* (Oxford University Press) became a cornerstone for researchers in population biology, conservation biology and landscape ecology. He identified the genetic basis of traits that underpin survival in fragmented habitats. Most recently, he demonstrated with colleagues that an increasing prevalence of inflammatory diseases is associated with declining biodiversity.

Hanski, who died on 10 May, was born in 1953 in Lempäälä, Finland. As a child he collected butterflies at his grandparents' house in southeastern Finland. Decades later, Hanski reflected that many of his most successful research projects were inspired by these outdoor adventures and by the encouragement that he received from Esko Suomalainen, a geneticist at the University of Helsinki whom he had contacted after finding a rare butterfly at his grandparents' house.

Hanski studied biology at the University of Helsinki and gained his doctorate, on the community ecology of dung beetles, from the University of Oxford in 1979. He found that most dung-beetle species clump together, with particular species common in some pats but scarce or absent in others.

Before the 1970s, ecologists paid little attention to whether populations were distributed continuously or in many local patches or both. Throughout his career, Hanski was intrigued by the ecology and evolution of species found in islands — naturally fragmented habitats. In 1969, population biologist Richard Levins introduced the concept of a metapopulation — a 'population of populations' — species living in networks of habitat patches such as cowpats or islands, work that Hanski built on.

Returning to Helsinki after his doctorate, Hanski continued to develop models for metapopulation survival. By the late 1980s, he was ready to test his predictions in the field, but which insect to study, and where? He was inspired during a fortuitous visit by renowned population biologist Paul Ehrlich of Stanford University in California. Discussions about Ehrlich's research on Edith's checkerspot butterfly (*Euphydryas editha*) prompted Hanski

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to choose the Glanville fritillary butterfly (*Melitaea cinxia*) in the Åland Islands off southern Finland to test his predictions.

In the early 1990s, he set out to map all suitable habitat patches for *M. cinxia* in Åland. His effort has grown into a database of more than 4,000 localities. These places are checked each year for *M. cinxia* and its larval host plants — as well as the parasitoids and pathogens of each.

This has since become one of the most important model systems in population biology. A one-of-a-kind long-term data-collection effort, it is revealing how species and their interactions are responding to climate change, as well as shedding light on how species cope with habitat fragmentation.

In 1994, Hanski published the incidence-function model, which elegantly formulated the relationships between the area and isolation of a habitat patch and the likelihood of it being occupied by a species (I. Hanski *J. Anim. Ecol.* **63,** 151–162; 1994). This launched a new era of spatially explicit population models and was quickly adopted by ecologists.

Those of us who worked with Hanski will remember his sharp intellect and ceaseless enthusiasm for understanding nature. He was quick to adapt new methods and techniques. The Metapopulation Research Centre in Helsinki that Hanski established in 2000 consists of ecologists, evolutionary biologists, mathematicians, bioinformaticians and molecular biologists. Hanski also led Finland's first sequencing of an animal or plant genome: that of his Glanville butterfly, published in 2014 (V. Ahola *et al. Nature Commun.* **5,** 4737; 2014).

In 2003, nearly 25 years after completing his thesis, Hanski returned to his beloved dung beetles. He launched a project in Madagascar to study the evolutionary biology of the island's diverse endemic species of dung beetle and how these ecologically crucial communities respond to habitat loss. He led a series of excursions to Madagascar to work with local students, his team from Finland and his family. These trips became legendary, both for their scientific value and for the camaraderie he fostered.

Among numerous honours, Hanski was awarded ecology's top gong, the Crafoord Prize in Biosciences, in 2011. And despite his hectic schedule, he always prioritized public engagement. In Finland, Hanski was known for his views on conservation, in particular the protection of old-growth forests. Hanski was also a powerful advocate for basic research, criticizing science policy that demanded immediate economic benefit and arguing that such short-sighted aims threaten the fundamental process by which knowledge is generated.

Training young scientists was a top priority. Always keen to discuss ideas and offer feedback on manuscripts, Hanski became a co-author only on papers on which he felt he had made a significant intellectual contribution. This policy promoted the independence of early-career scientists working in the Metapopulation Research Centre. He loved to debate, and challenged everyone — regardless of their career stage — to discuss topics ranging from science to society.

Ilkka lived in Helsinki with his wife Eeva Furman, a professor of environmental policy, and three children. He was dedicated to his family, a quality that resulted in a family-friendly working environment in the centre. After being diagnosed with cancer in 2014, Ilkka, with typical determination, completed projects closest to his heart — notably a book, *Messages from Islands: A Global Biodiversity Tour*, to be published in December.

Ilkka had so much more to give and he touched so many in the ecology community. His death leaves a gap that won't be filled. ■

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