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Ilkka Hanski: The legacy of a multifaceted ecologist

Preface

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The exceptionally talented and versatile ecologist Ilkka Hanski passed away on 10 May 2016. Ilkka Hanski's work has been widely acknowledged. Amongst the others, he received prestigious Crafoord's prize in 2011, and an honorary title of Academician of Science from the Academy of Finland in 2015. Alongside his research career, Ilkka Hanski actively participated in debates on social issues, especially regarding conservation policies in Finland, his native country. He was elected a member of the Board of the University of Helsinki in 2014, and in his essay (Hanski 2016), he fiercely criticized Finnish Government's unprecedented cuts of research and university funding, undermining the future of Finnish science.

Ilkka Hanski was a prolific researcher and his works are well known and cited globally. He was also an active supporter of the scientific community in Finland, writing to many journals published in Finland. In *Annales Zoologici Fennici* (AnZF) he published 20 articles and was a member of its Editorial Board in 1993–2015. His first publication in the journal, with Hannu Koskela (Koskela & Hanski 1977), started his long series of papers on dung beetles; while the last one, with Varpu Mitikka (Mitikka & Hanski 2010), was on the genetic basis of dispersal in metapopulations. Among others, Ilkka Hanski published his first article on extinction debt in AnZF (Hanski 2010), which became his most cited publication in AnZF and all time fifth most cited publication in the journal to date. Hanski also guest-edited two special issues for AnZF, one on ecological significance of spatial and temporal variability (Hanski 1988), and one on population biology of Eurasian shrews (Hanski & Pankakoski 1989).

Throughout his career Ilkka Hanski worked in many fields of ecology. His contributions to each stand out, due to his insightful integrative research, his accessible communication of ideas, and because of the value he placed on mentorship and collaboration. This combination of strengths resulted in his having real impact on the direction and vitality of much ecological research, and on the work of many individual researchers.

In this volume we bring together 21 papers by researchers who worked with Ilkka Hanski at different points of his career, on the topics of ecology, evolution and conservation. In the process of putting together this volume we, the editors, have witnessed the great admiration, appreciation and goodwill that the authors and reviewers involved have for Ilkka Hanski. We thank them for their work.

After a preface written by Eeva Furman, who was Ilkka's wife, which portrays the rich integrations of Ilkka's childhood interest in nature, his family life and his scientific career, the papers in this issue are organized into five sections. The first, *Conservation policy and the value of biodiversity*, pays tribute to Ilkka Hanski's strong support of conservation. Ilkka is well known for his groundbreaking work on how biodiversity is maintained, or not maintained, in a landscape. This angle, and its value internationally, is presented in the first paper by Paul Ehrlich, leader of the *Center for Conservation Biology* at Stanford University. In Finland Ilkka Hanski has been a strong voice advocating conservation

of forests and the value of biodiversity locally. Janne Kotiaho draws on that in his essay on conservation and sustainability, and the Finnish forest-policy. Janne Kotiaho and Mikko Mönkkönen then point out that conservation biologists should take the long view by conserving even degraded habitats that may have little value now, but may become valuable in future. In the final paper of that section, Ilkka Hanski's more recent view on the positive association of environmental biodiversity, environmental microbial diversity, and human microbiota with human health is presented by his collaborators, led by Lasse Ruokolainen.

The remaining sections of the special issue concentrate on more basic research, much of which underpins the conservation biology presented above. In the *Community ecology* section, Susan Harrison ponders the value of landscape connectivity for the integrity of specialized serpentine plant communities in the western United States. The other two papers address spatially structured communities by exploring interactions among species. Bob Holt's paper approaches it conceptually through mathematical modelling. Marko Nieminen and Saskya van Nouhuys present an empirical study of the relative importance of spatial structure and trophic interactions for the composition of an insect community.

Ilkka Hanski developed the theory of metapopulation ecology by using relatively simple mathematical models to show the impact of habitat fragmentation on populations. For this he used real long-term data from natural terrestrial populations distributed over landscapes. The first paper in the *Metapopulation ecology* section, by Oscar Gaggiotti, approaches the challenge of applying metapopulation theory to marine systems in which connectivity, the lynchpin of the metapopulation theory, is complicated by large-scale movement of propagules in ocean currents. The two following papers are focused on modelling other aspects of dispersal. The one by Otso Ovaskainen integrates the effect on metapopulation dynamics of dispersal *per se* with local population dynamics. In the next, Samuel Soubeyrand and Anna-Liisa Laine address group dispersal which, for species such as fungi that disperse in clumps of spores, should decrease the negative impact of the Allee effect in newly colonized patches. In the final paper in this section, Tadeusz Kawecki develops a metapopulation model involving two topics of Hanski's long-standing interest: coexistence of competing species and local adaptation in metapopulations.

The set of papers in the *Population ecology and life history* section pay tribute to the value Hanski placed on deeply understanding species in their environments, and on using that information to build ecological theory. The papers include studies of species in Finland that were near and dear to Hanski's heart, such as the population dynamics of shrews and voles by Heikki Henttonen *et al*., the three-toed woodpecker by Timo Pakkala *et al*., and two papers about the life history of the Glanville fritillary butterfly, first by Mikko Kuussaari and Michael Singer, and second by Singer *et al*. Alexander Krowiak *et al*. show the complexity of resource limitation (soil nutrients *vs*. arthropod prey) for a carnivorous plant in Iceland. Finally Ilkka's interest in modelling life history evolution in ecological settings is represented by Mats Gyllenberg *et al*.

Ilkka Hanski's interests in population dynamics and biodiversity drove him to become interested in the interplay between ecological and evolutionary processes. The first paper in the *Genetics and evolution* section, by Tanjona Ramiadantsoa *et al*., addresses evolution on the large scale by modelling geographic radiation of species using phylogenetic information. The next paper, by James Davies and Ilik Saccheri, looks on a smaller scale at adaptive evolution, within a species, of phenotypic plasticity in an empirical system. The last two papers focus on the genomics of the Glanville fritillary butterfly: Kristjan Niitepõld and Marjo Saastamoinen bring together the work started in the early 2000s by Hanski and others on the phosphoglucose isomerase (*PGI*) gene, showing the consistent effort, valued greatly by Hanski, to tie genetics patterns to the ecological context in which they are found. The final paper, by Virpi Ahola *et al*., place the genome of *Melitaea cinxia*, which Hanski and colleges began to construct in 2009, when there was little knowledge of genomes of non-model species, in the context of other butterfly genomes.

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