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Ilkka Hanski: The legacy of a multifaceted ecologist

What should conservation biologists be doing? An homage to Ilkka Hanski

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It is a pleasure and an honor to dedicate this paper to my old friend and colleague Ilkka Hanski, whose work on populations and metapopulations has been so central to conservation biology.

While the accelerating loss of biodiversity has been given increasing attention recently from the biological community (Barnosky *et al*. 2010, Ceballos *et al*. 2015a, 2015b, Cronk 2016, Maxell *et al*. 2016), the general public is not well informed about it. This could be a side effect of the media-generated view that environmental problems are not all that important — with the possible exception of anthropogenic climate disruption. This was dramatically demonstrated in the 2016 Presidential elections in the United States in which there was almost no debate on the existential threat those problems posed to human health and well-being, indeed to the persistence of civilization. Worse yet, the new Trump administration shows every sign of deliberately speeding the destruction of biodiversity and thus speeding a collapse of civilization. But it is also clear from the activities of conservation biologists (including many ecologists, evolutionists, and behaviorists) that their training needs to be modernized, and as a result too much of their research is likely a waste of time.

Part of the problem traces to an innocent act by my hero, Charles Darwin, the greatest biologist who ever lived. He titled his magnum opus *On the Origin of Species*. Our attempts to preserve biodiversity today might be simpler if he had called it *On the Differentiation of Populations*. It has long been evident that species were simply arbitrary segments of a differentiating tree of life: populations showing various degrees of difference from other populations, but being distinct enough for a taxonomist to think of them as "different kinds." This has become super-evident in recent years as molecular phylogenies of recent radiations (e.g., Moyle *et al*. 2009) show continuous degrees of differentiation of populations, just as one would expect. That makes it clear that the whole "what is a species?" literature is nonsense — the intellectual equivalent of geologists perpetually trying to define a "mountain." Are Lhotse and Nuptse different mountains or submountains of Everest? The instructive thing about the species debate, which has persisted to this day half a century after the issue was basically settled (Ehrlich 1961, Sokal & Crovello 1970), is how unnecessary the fuss has been (Ehrlich *et al*. 2004: 297) and how much human brains like to fraction continua into discrete categories (think colors). For communication "species" and "population" — like "mountain" and "hill" and "red" and "yellow" — are useful and easily understood even though they are segments of continua and impossible to satisfactorily define.

The consequences of Darwin's title for conservation have been profound. It has focused attention on the relatively slow rate of species extinctions [even when greatly accelerated during mass extinction events (Ceballos *et al.* 2015b)] rather than on the much more serious and dramatic crisis of "population extinctions" (Ceballos *et al.* 2017), the extirpation of entities less distinct than those designated "species." This erroneous emphasis has been typical of the conservation community; extinctions of populations has gotten relatively little attention even from those who should know better (like me!). Anne and I subtitled our book on extinction *The Causes and Consequences of the Disappearance of Species*, and we pretty much ignored population extinctions (Ehrlich & Ehrlich 1981). So the first thing I would recommend conservation biologists to do is to shift their focus from species extinctions to "population extinctions and declines" so as to emphasize the systematic level where loss is most obvious and most immediately damaging. Overall, they should stop worrying over whether an entity to be preserved is a "good species" (nauseating term), subspecies, population of hybrid origin, metapopulation, or entire ecosystem (Morell 2016).

When conservation biologists do research in the field, their first priority should be to start long-term studies that will eventually give science a better grasp of the dynamics of populations and metapopulations, and thus of the patterns of population extinction. Such information will be very useful if global society should ever decide to make a serious effort to avoid collapse and preserve biodiversity — and in so doing maintaining ecosystems processes critical to human beings, particularly at the local level. It was, after all, long-term investigations that originally brought the whole topic of population extinction to the fore (Ehrlich & Hanski 2004), and ignited the field of metapopulation ecology that Ilkka Hanski did so much to develop (e.g., Hanski & Gilpin 1997, Hanski 1999, 2001). Studies of metapopulations have done much to inform scientists on the scope and magnitude of population extinctions.

Whatever were the original questions that stimulated the initiation of long-term studies, the payoffs have almost always been impressive for conservation biology. For example, decades of studies of yellow-bellied marmot populations (Armitage 2014) have shown that those rodents can survive in a very wide variety of habitats through an altitudinal gradient of some 2000 m and so appear to be resilient to climate disruption. But similar data for other marmot species would be most helpful in forecasting the fate of rodent communities under climate disruption, as multi-species studies have been in desert rodent communities (e.g., Thibault *et al.* 2010).

New long-term studies are not always essential, however, when detailed historic data sets are available for comparison. A classic example of the latter is a study of plant-pollinator interactions in a midwestern U.S. deciduous forest understory. The system was first studied at the end of the 19th century. Laura Burkle and her colleagues (Burkle *et al.* 2013) redid the study recently and discovered that in ~120 years the plant-pollinator network had been disrupted by many factors, including extinction of half of the bee populations originally involved. At a much less detailed level, I was able to extract evidence of extensive population extinctions since 1940 from "square-bashing" censuses of British butterflies (Ehrlich 1995). In Lepidoptera, the order of insects most attended to by naturalists, records showing their decimation in Europe goes much further back (Habel *et al.* 2015, Thomas 2016). But considering the obviously huge scale of the problem, detailed information on the past (or even present) dynamics of populations is rare indeed, and one result has been an underestimation of the rate of decay of biodiversity. We are largely dependent for understanding the scale of the problem on records of species range shrinkage (Ceballos *et al.* 2017).

But that does not include another problem in tabulating extinctions, especially population extinctions. It is that of "Zombies" — populations or species that are counted as extant but have so few individuals left or so little habitat remaining that they can no longer play an important role in an ecosystem and are doomed to extinction. They are the "living dead," in Janzen's (2001) parlance. Ilkka Hanski, who also used the term, was instrumental in bringing the metapopulation version of this problem to attention (Hanski & Ovaskainen 2002). This means that many estimates of extinction rates are deceptively low. This is especially so in plants (Cronk 2016). Think of the "specimen" rainforest trees, left growing isolated in tropical pastures to give shade for livestock. Such long-lived individuals may survive for decades, but without hope of reproducing as there is no habitat for their offspring (Janzen 2001). Plants in general are more likely to become zombies than animals. Besides having a long life-expectancy, they can also leave seed banks that last for years, producing relaxation times of even centuries (Diamond 1972) and a huge "extinction debt" (Tilman *et al*. 1994) before the final mature individuals pass from the scene.

Then, of course, what may be the easiest thing for conservation biologists to do is avoid silly internal battles. An especially senseless example was the recent dispute between some who focused their approach to conservation on preserving ecosystem services and others who thought it wiser to emphasize the ethical need to preserve our only known living companions in the universe. With most of humanity engaged in a ruthless and all-too-successful war of extermination (Ceballos *et al*. 2017), most conservation biologists fortunately seem to realize that a diversity of approaches to saving it (and ourselves) is demanded; whatever works (Tallis *et al*. 2014). The armies of extinction are much better organized and funded, however, and disputes over the tactics of conservation do not help achieve agreed-upon goals.

But, in my view, the most important change for the discipline is for all conservation biologists to be at the leading edge of efforts to inform decision makers and the public about the basic drivers of the annihilation of nature (Ceballos *et al*. 2015a). Those are, of course, human overpopulation and continuing population growth, overconsumption by the rich, and perpetuation of gross economic and social inequities. Human beings compete with other organisms for energy, space, water, and many other basic resources (Vitousek *et al*. 1986); therefore the more people there are, the greater the eco-holocaust. This is not just an issue of the wiping out of rhinos, elephants, gorillas, great whales, and the like. For example, habitat destruction as human populations expand, urbanize, and convert natural areas to agriculture has inexorably wiped out populations of butterflies over much of the globe, one of the few kinds of invertebrates to which people pay attention. In the hot-spot state of California this has been well-documented (e.g., Connor *et al*. 2002). I well remember seeing a map in the American Museum of Natural History of the Los Angeles area, showing the favorite collecting spots in the 1920s of a well-known lepidopterist, J. D. Gunder. By the 1950s they were all under concrete. Recently it has been shown that even in Los Angeles' giant Griffith Park (> 1700 ha next to Hollywood), all populations of ten species historically present have gone extinct, as well as, doubtless, many populations of other species that have not yet disappeared entirely from the Park.

Urban areas are quite naturally one of the front lines of the annihilation, often losing their populations of the rarer, more specialized, more naturally scattered species first (e.g., Fattorini 2011). These direct impacts of human expansion and habitat destruction are easily understandable and ongoing on a vast and complex scale as more than half of *Homo sapiens* is now urbanized (Satterthwaite *et al*. 2010), and feeding a growing population seems to demand further increasing humanity's already vast, biodiversity reducing agricultural activities (Maxell *et al*. 2016). Perhaps even more important, if less easily comprehended, is the indirect anthropogenic assault on biodiversity launched through climate disruption and global toxification.

As was clear long ago, rates of extinction are tightly attached to the scale of the human enterprise (Ehrlich 1995). That scale is continuing to increase, and a recent estimate is that roughly 58% of all "wildlife" (14 152 monitored populations of 3706 vertebrate species) was wiped out between 1970 and 2012 (*see* http://bit.ly/2ePXWb9). This dismal statistic further supports the notion that Earth is undergoing an eco-holocaust, and that it is far from limited to iconic mammals and butterflies. Also worrying, for instance, are reports of steep declines in "common" species of North American birds (*see* http://bit.ly/2a1QWU8).

The bottom line, then, is that all conservation biologists should be speaking out on issues of public policy, working hard as citizens to humanely reduce the scale of the human enterprise (Ehrlich *et al*. 2012) and deal with the complex of existential problems we know as "the human predicament." The standard approach of citing projected human population figures in scientific papers as if they are exogenous variables handed down from heaven and not susceptible to change through human action must end. It is a fiction that must be exposed — before anthropogenic changes in death rates clarify it for even the most obtuse. It is far too late to leave to politicians or the general public the monumental task of avoiding a collapse of civilization (Ehrlich & Ehrlich 2013). In addition, no one certainly should take the position that a collapse might be a good thing, taking the pressure off for the non-human parts of the biosphere. If the collapse involves a large-scale nuclear war, as is all too possible (Perry 2015), the results could be as catastrophic for the rest of biodiversity as for humanity.

Conservation biologists should be as involved as possible in public discourse over policy issues where their expertise is pertinent (Hanski 2002). Being a scientist does not debar one from acting as concerned citizens — as Ilkka demonstrated both in print and in person. They should be at the front lines of the fight for equal rights for women in all societies, universal access to modern contraception, availability of safe back-up abortion, and other measures known to lower fertility rates. Similarly, conservation biologists should be pioneers in seeking ways to reduce economic and other inequities and reduce consumption among the already rich. To do otherwise is to give up on conservation and face the fact that most of our other battles, to outlaw transport of endangered species, to protect individual endangered organisms, to set up reserves, to harvest sustainably, are at best only delaying actions. Conservation biologists must continuously remind the public and decision makers that continuous growth is the "creed of the cancer cell."

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References

Armitage, K. B. 2014: *Marmot biology: sociality, individual fitness, and population dynamics*. — Cambridge University Press, UK.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B. & Ferrer, E. A. 2010: Has the Earth's sixth mass extinction already arrived? — *Nature* 471: 51–57.

Burkle, L. A., Marlin, J. C. & Knight, T. M. 2013: Plant–pollinator interactions over 120 years: loss of species, co-occurrence, and function. — *Science* 339: 1611–1615.

Ceballos, G., Ehrlich, P. R. & Dirzo, R. 2017: Biological annihilation via population loss and decline: The real sixth mass extinction. — *Science Advances*. [In press].

Ceballos, G., Ehrlich, A. H. & Ehrlich, P. R. 2015a: *The annihilation of nature: human extinction of birds and mammals*. — Johns Hopkins University Press, Chicago.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M. & Palmer, T. M. 2015b: Accelerated modern human-induced species losses: entering the sixth mass extinction. — *Science Advances* 1(5), e1400253, doi:10.1126/sciadv.1400253.

Connor, E. F., Hafernik, J., Levy, J., Moore, V. L. & Rickman, J. K. 2002: Insect conservation in an urban biodiversity hotspot: the San Francisco Bay Area. — *Journal of Insect Conservation* 6: 247–259.

Cronk, Q. 2016: Plant extinctions take time. — *Science* 353: 446–447.

Diamond, J. M. 1972: *Avifauna of the Eastern Highlands of New Guinea*. — Nuttall Ornithological Club.

Ehrlich, P. R. 1961: Has the biological species concept outlived its usefulness? — *Systematic Zoology* 10: 167–176.

Ehrlich, P. R. 1995: The scale of the human enterprise and biodiversity loss. — In: Lawton, J. H. & May, R. M. (eds.), *Extinction rates*: 214–226. Oxford University Press, Oxford.

Ehrlich, P. R. & Ehrlich, A. H. 1981: *Extinction: the causes and consequences of the disappearance of species*. — Random House, New York.

Ehrlich, P. R. & Ehrlich, A. H. 2013: Can a collapse of civilization be avoided? — *Proceeding of the Royal Society B* 80: 20122845, doi:10.1098/rspb.2012.2845.

Ehrlich, P. R. & Hanski, I. (eds.) 2004: *On the wings of checkerspots: a model system for population biology*. — Oxford University Press, Oxford.

Ehrlich, P. R., Hanski, I. & Boggs, C. L. 2004: What have we learned? — In: Ehrlich, P. R. & Hanski, I. (eds.), *On the wings of checkerspots: a model system for population biology*: 288–300. Oxford University Press, Oxford.

Ehrlich, P. R., Kareiva, P. M. & Daily, G. C. 2012: Securing natural capital and expanding equity to rescale civilization. — *Nature* 486: 68–73.

Fattorini, S. 2011: Insect extinction by urbanization: a long term study in Rome. — *Biological Conservation* 144: 370–375.

Habel, J. C., Segerer, A., Ulrich, W., Torchyk, O., Weisser, W. W. & Schmitt, T. 2015: Butterfly community shifts over

two centuries. — *Conservation Biology* 30: 754–762.
Hanski, I. 1999: *Metapopulation ecology*. — Oxford University Press, Oxford.
Hanski, I. 2001: Spatially realistic theory of metapopulation ecology. — *Naturwissenschaften* 88: 372–381.
Hanski, I. 2002: In the midst of ecology, conservation, and competing interests in the society. — *Annales Zoologici Fennici* 39: 183–186.
Hanski, I. & Ovaskainen, O. 2002: Extinction debt at extinction threshold. — *Conservation Biology* 16: 666–673.
Hanski, I. A. & Gilpin, M. E. (eds.) 1997: *Metapopulation biology: ecology, genetics and evolution*. — Academic Press, London.
Janzen, D. H. 2001: Latent extinctions: the living dead. — *Encyclopedia of Biodiversity* 3: 689–699.
Maxell, S. L., Fuller, R. A., Brooks, T. M. & Watson, J. E. M. 2016: Biodiversity: the ravages of guns, nets, and bulldozers. — *Nature* 536: 143–145.
Morell, V. 2016: Rethinking the North American wolf. — *Science* 353: 434–435.
Moyle, R. G., Filardi, C. E., Smith, C. E. & Diamond, J. 2009: Explosive Pleistocene diversification and hemispheric expansion of a "great speciator". — *Proceedings of the National Academy of Sciences of the USA* 106: 1863–1868.
Perry, W. J. 2015: *My journey to the nuclear brink*. — Stanford University Press, Stanford.
Satterthwaite, D., McGranahan, G. & Tacoli, C. 2010: Urbanization and its implications for food and farming. — *Philosophical Transactions of the Royal Society B* 365: 2809–2820.
Sokal, R. R. & Crovello, T. J. 1970: The biological species concept: a critical evaluation. — *American Naturalist* 104: 127–153.
Tallis, H., Lubchenco, J., Adams, V. M., Adams-Hosking, C., Agostini, V. N. & Kovács-Hostyánszki, A. 2014: Working together: a call for inclusive conservation. — *Nature* 515: 27–28.
Thibault, K. M., Ernest, S. M., White, E. P., Brown, J. H. & Goheen, J. R. 2010: Long-term insights into the influence of precipitation on community dynamics in desert rodents. — *Journal of Mammalogy* 91: 787–797.
Thomas, J. A. 2016: Butterfly communities under threat. — *Science* 353: 216–218.
Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. 1994: Habitat destruction and the extinction debt. — *Nature* 371: 65–66.
Vitousek, P. M., Ehrlich, P. R., Ehrlich, A. H. & Matson, P. A. 1986: Human appropriation of the products of photosynthesis. — *BioScience* 36: 368–373.