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Richard S. Gomulkiewicz (1962–2023)

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Incisive theoretical population geneticist.

Richard Stephen Gomulkiewicz (Dick to his family and many friends) had a zest for life and learning, and used crisp reasoning and mathematics to shed light on deep and abiding questions in ecology and evolutionary biology. On 25 March 2023, after a short illness, he passed away in peace in Lewiston, Idaho, surrounded by his loving family. This is a grievous loss of an outstanding scientist and empathetic human being. Dick was a remarkable person in his personal life and throughout his career. He made fundamental and lasting contributions to evolutionary theory — in particular, at its interface with ecology. He tackled complex problems, such as the evolution of phenotypic plasticity, the role of evolution in modulating interspecific interactions and extinction, and the evolutionary dimensions of gene drive. Dick was a deep, serious thinker who pondered challenging problems whose resolutions required real intellectual depth and creativity. His well-crafted papers are models of rigour and have true staying power, reflecting both his mathematical acumen and his grounding in empirical biology.

Dick Gomulkiewicz was born 26 February 1962 in Wilkinsburg, Pennsylvania, and moved around the world with his family, finally settling in Wenatchee, Washington. Throughout his life, all who encountered him were struck with his ironic sense of humour, sharp intelligence, non-judgmental character and sense of fun (he once starred on the trapeze in a youth circus). Dick was exposed to applied ecological science as a young man, working on biocontrol of agricultural pests, and later as a student applying genetic tools to identify the origins of harvested salmon — whether they were from hatcheries or instead from endangered natural populations. His contributions to evolutionary theory were firmly grounded in an appreciation of ecology and natural history. His keen interest and talent in mathematics led him to receive his undergraduate degree in mathematics from Washington State University in 1984 (where he met his wife, Susan), followed by doctoral studies in applied mathematics and population ecology with one of us (A.H.) at UC Davis, developing models of sexual selection given limited mate choice. Dick then had a postdoctoral fellowship at the University of Texas, where he started to develop an influential body of ideas on the evolution of norms of reaction. In 1991, he accepted his first faculty position at the University of Kansas. While there, he struck up a friendship and fruitful professional collaboration with another of us (R.D.H.) and M. Barfield, which lasted until his death. In 1996, he moved back to Washington where he took positions at Washington State University, collaborated with colleagues (including S.L.N.) and remained with his family there for the rest of his life.

Dick's postdoctoral work on the evolution of reaction norms sparked a lifelong interest in phenotypic plasticity. His earliest paper on this theme (R. Gomulkiewicz & M. Kirkpatrick, *Evolution* **46**, 390–411; 1992) laid out a general quantitative genetics framework for understanding the evolution of trait responses to changing environmental variables. This work demonstrated that genetic constraints could lead to divergent evolutionary equilibria for different patterns of environmental variation. His abstract characterization of phenotypic plasticity in terms of 'function-valued' traits — in which phenotypic expression varies along a continuum, such as age — is a conceptually profound and biologically rich insight. A recent review (R. Gomulkiewicz et al., *Ann. Rev. Ecol. Evol. Syst.* **49**, 139–164; 2018) made a compelling argument that 'curve-thinking' (in which functions replace singular trait values as the object of evolutionary analyses) provides a powerful tool for addressing a wide range of evolutionary questions, including clarifying the nature of constraints in evolution by natural selection. Dick's final published paper (R. Gomulkiewicz & J. R. Stinchcombe, *Am. J. Bot.* **109**, 1519–1524; 2022) laid out a coherent framework for future evolutionary studies of plasticity that will be drawn on for many years.

After moving to the University of Kansas in 1991, Dick began working with one of us (R.D.H.) and M. Barfield on problems at the interface of ecology and evolution. This work examined how evolution moulds the niche of a species, especially in conditions in which a population experiences an abrupt environmental stress. The first paper on this theme (R. Gomulkiewicz & R. D. Holt, *Evolution* **49**, 201–207; 1995) used models of coupled evolutionary and demographic dynamics to characterize 'evolutionary rescue' — when evolution operates sufficiently fast to enable numbers to rebound after an initial period of decline. This paper led to a fruitful research programme for the rest of

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Dick's career. The rich array of themes that Dick examined included: evolution in 'sink' populations maintained by recurrent immigration from sources; the role of phenotypic plasticity in rescue; the influence of stage structure (M. Barfield et al., *Am. Nat.* **177**, 397–409; 2011 — a paper that won the Presidential Award as the best paper published in the journal that year); and effects of density dependence and temporal environmental variability. Dick began to develop a general theory of the interplay between demographic and genetic constraints in evolution (R. Gomulkiewicz & D. Houle, *Am. Nat.* **174**, E218–E229; 2009), a topic in which he was actively engaged up to his final illness. Drawing on his early experience with applied ecology, Dick related abstract evolutionary rescue ideas to concrete problems, such as eliminating noxious agricultural pests or human pathogens, gauging the effect of introgressive hybridization on species persistence, and assessing how evolution modulates the establishment of invasive species. Through his intellectual leadership, Dick had a central role in evolutionary rescue becoming a 'growth industry' in applied evolutionary biology in recent years.

After moving to Washington State University, Dick worked with two of us (S.L.N. and R.D.H.) and others (particularly J. N. Thompson) to formalize the geographic mosaic theory of coevolution. In a series of papers, starting in 1999 (S. L. Nuismer et al., *Proc. Royal Soc. B* **266**, 605–609; 1999) and culminating in 2007 (R. Gomulkiewicz et al., *Heredity* **98**, 249–258; 2007), Dick and his collaborators laid out concrete guidelines for testing the geographic mosaic theory. This work provides an essential conceptual framework for developing rigorous studies of coevolution in spatial contexts. In recent years, Dick (in collaboration with J. Bull, S. Krone and others) had begun to develop incisive theory that aimed at understanding the factors that might permit (or preclude) the evolution of resistance to gene drive — a rapidly developing technology to control pests and pathogens. A true hallmark of all his theoretical contributions is their clear grounding in empirical field and laboratory biology.

Dick, through his persona, infused all his collaborations with a special grace, providing a kind of Platonic ideal of scientific collaboration. He brought a sense of fun and joy to all of his colleagues and collaborators, many of whom became his lifelong friends. We feel fortunate to count ourselves among those friends. Beyond the vital intellectual contributions that Dick made to research efforts, he was a real pleasure to work with and, in the old Yiddish term, embodied a true *mensch* in his interactions with everyone — faculty, students and non-academics. He provided a model of work–life balance, putting his deep love for his family above everything else, and he delighted in cycling, reading broadly and listening to music of all sorts. Dick Gomulkiewicz's steadfast, warm friendship will be missed by his many friends, but through them and the pages of his publications, his vital contributions to evolutionary biology will live on.

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Additional information

R.D.H. was a frequent collaborator of Dr Gomulkiewicz at the University of Kansas and later when Dr Gomulkiewicz moved to Washington State University. A.H. was the doctoral advisor of Dr Gomulkiewicz at UC Davis. S.L.N. had Dr Gomulkiewicz as his doctoral thesis advisor, and in subsequent times was a colleague and frequent collaborator of Dr Gomulkiewicz at Washington State University.