Edward Wilson: The Lord of the Ants*

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Edward Wilson, a leading myrmecologist of the century, made a substantial contribution to the science of ant taxonomy. He pioneered the concept of new systematics in ant taxonomy, advocating a comprehensive viewpoint about species delimitation.

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Introduction

"In natural history, addiction occurs early"; this is what Edward Wilson wrote in a memorial tribute to William L. Brown. Ed himself was no exception and admitted, "...I was 18 (in 1947) and already taken my vows, so to speak, in ant taxonomy". After earning his BS and MS degrees in 1950 from the University of Alabama, Edward Wilson started exploring ant collection with Bill Brown at the Museum of Comparative Zoology at Harvard. The taxonomic practice at that point in time lacked the foresight of evolutionary thought. It revolved around identification and naming, without the exact quantification of variations in isolated populations. Individuals/specimens/populations were classified as subspecies of a particular species based on the comparison (of certain morphological characters) with type specimens (standard specimen thought to be representative of a species and on which the original description of the species was based). Therefore, if there was variation within a species, a specimen that differed from a type specimen might be classified as a different variant. In Linnean taxonomy, species are classified using the binomial nomenclature—the system of naming in which two terms are used to denote a species of a living organism, the first one indicating the genus and the second being the specific epithet. Therefore, the

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practice of relying on the type specimen (typological thinking in the context of taxonomy) led to taxonomic chaos, mostly resulting in trinomial nomenclature (with names of the genus, species, and subspecies) wherever geographic variation was encountered.

Ernst Mayr had already come up with the idea of the 'biological species concept', according to which species were envisioned as groups of interbreeding populations, reproductively isolated from other such groups. Confronted with typological thinking and frequent application of trinomial nomenclature, Wilson and Brown (1953) comprehensively wrote about the concept of the subspecies and its taxonomic usage, suggesting that the use of subspecies in taxonomy be abandoned [1]. They instead helped to establish Mayr's criterion for species (interbreeding populations) as objective and relevant for taxonomic work. Their arguments about the quantification of variation in geographically isolated populations were well received by biologists; as Brown stated later, "The success of a paper on geographical subspecies by Edward Wilson and me was exhilarating enough to set off a train of what Wilson called *megathought* discussions over a wide range of evolutionary topics". On Brown's persuasion, Wilson had selected the taxonomic revision of the Holarctic ant genus *Lasius* (*Figure* 1) as the subject of his doctoral thesis [2]. The duo had many discussions on the finding that certain pairs of species in the genus *Lasius* were morphologically and ecologically distinct whenever they occurred in sympatry (in the same place at the same time, resulting in the possibility of interaction). But when the same species were encountered allopatrically (in different geographic areas), the distinct morphological and ecological traits were not so pronounced. Instead, the allopatric populations' characteristics appeared to be intermediate to, or a blend of, the two species in sympatry. Brown and Wilson analysed this phenomenon in a larger framework, along with a body of evidence from previous literature and field studies, and termed the phenomenon 'character displacement'. Characters, which are morphological or ecological traits, were proposed to be different between the same species in sympatry but not in allopatry, due

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Figure 1. Ant of genus *Lasius*, the taxonomic revision of which Wilson worked on for this doctoral thesis.
(Image attribution: Photograph by April Nobile available under Creative Commons license CC BY 4.0 from https://www.antweb.org/specimen/CASENT0005404 (AntWeb. Version 8.78. California Academy of Science, online at https://www.antweb.org, Accessed 28 July 2022).

to isolating mechanisms and competitive divergence. Isolating mechanisms are ways in which reproduction between individuals of different species is prevented or reduced. Competitive divergence is the divergence of characters between sympatric species due to an increased competition being encountered if they have similar characters. Brown and Wilson (1956) wrote: "... if populations of closely related species are different, where they occur together, species occurring apart in isolation do not have to be different" [3].

These findings, when viewed in the larger context, provided an altogether different perspective to taxonomists for the analysis of traits used in species delimitation (the assignment of specimens to the same or to different species). A different perspective was also provided to naturalists, as well as evolutionary biologists, to think in terms of trait evolution in response to different selection pressures. Furthermore, the *Lasius* monograph discouraged the use of subspecies names as large population sizes would be required to correctly quantify intraspecific variation, which was not being done previously. Morphometric measurements, in-

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dices, and certain traits like pilosity (the presence/arrangement of long, thicker hair) were comprehensively used in species delimitation, which laid the foundation for modern ant taxonomy. Wilson attempted provisional phylogeny (evolutionary history) of the genus, and that has recently been revisited by Brendon and co-workers (2022) by integrating molecular and morphological systematics [4]. On a personal note, Brendon stated, "Wilson's work on *Lasius* serves as a reasonable marker for the shift in ant taxonomy from the early typological works of the late 19th to the early 20th century to the population-thinking of the modern evolutionary synthesis. His consideration of the process of speciation reflects the careful accounting of variation within and among populations from the perspective of reproductive isolation (the "biological species concept"); this allowed Wilson to both trace geographic variation and to dispose of the trinomial and more-nomial systems that plagued earlier systematists. This cemented the trend in ant taxonomy of abandoning subspecies and finer categories, which remains a substantial issue to the present day. More broadly, Wilson also proposed an explicit phylogenetic hypothesis for the species of the genus, which had not been done within the subfamilies of ants since Carlo Emery's classic works in *Genera Insectorum*. Wilson's phylogenetic hypothesis and his classification of *Lasius* have served as the foundational work on this important Holarctic genus for over a half century, and has yet to be meaningfully updated in the Nearctic region, despite intense interest. The work remains essential to the present day for *Lasius*, and has been used in one way or another in studies of ant taxonomy globally, whether explicitly or not: His diagram for the inclination of hairs alone is a highly cited system. It is difficult to foresee a time when Wilson's work will have outlived its use".

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Edward Wilson travelled widely across the tropics, including the South Pacific, Australia, New Guinea, Fiji, New Caledonia and Sri Lanka. His taxonomic analysis of ants of these regions coupled with natural history is a treat to read. He provides an explicit account of ecology, evolution, and speciation patterns. His treatment of ants of Melanesia is a masterpiece, wherein he elaborates

upon the geographical variations seen in ant species to further discourage the use of subspecies nomenclature, as he and Brown had written earlier. Wilson emphasized that in order to understand biogeography and speciation patterns, revisionary taxonomy is a basic requirement. All of Wilson's research embodied taxonomic analysis, on which hypotheses were built. To understand the complexity of an organism, we ought to understand its natural relationships and interactions with other organisms. His preliminary observations of the zoogeography of Melanesian ant fauna (Ponerinae) were focused on adaptive shift and dispersal (species or populations adapt to marginal habitats around the original land mass, followed by colonization of new areas) [5]. He hypothesized that most of this Melanesian ant fauna has been derived from Oriental stock. Later, he expanded the view further with more data and concluded that a taxon maintains its place in a given land mass, undergoes expansion and contraction cyclically or else declines to extinction. This was referred to as the 'taxon cycle' [6]. This phenomenon has been found not only in ants but also in birds, and formed an important part of the 'theory of island biogeography', which Wilson proposed along with Robert MacArthur.

Another significant contribution by Wilson included the taxonomic revision of army ants (*Dorylus* and *Aenictus*) of the Indo-Australian area in 1964. He provided a detailed account of their biology and his viewpoint on their phylogeny, besides attempting to use numerical taxonomy. Numerical taxonomy involves using numerical methods (rather than qualitative assessments) such as cluster analysis on different characters in order to group together different taxa. This was followed by a detailed taxonomic account of the ants of Polynesia [8]. He also described socially parasitic ants and provided an analysis of the parasitic syndrome [9].

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Wilson, along with Brown, provided an elaborate view of the evolution of Dacetine ants [10]. His pursuit of ant systematics also included discoveries of fossil ants. A commendable contribution to ant systematics appeared in 2003, when Wilson revised the hyperdiverse ant genus *Pheidole* from the New World [11]. He

untangled the chaotic classification, which plagued the taxonomy of this genus, by characterising 625 known species, 341 of which he discovered as new to science! This voluminous contribution includes notes on the natural history of the species, drawings and keys to supplement their prompt identification.

Besides ant taxonomy and natural history, Wilson had an incredible interest in the evolution of social behaviour, physiology, biology, and chemical ecology of ants. The information gathered over the years appeared in the form of an all-inclusive treatise, *The Ants*, which remains a masterpiece in the field of myrmecology [12]. To many, Edward Wilson is known as a scientist, who promoted the cause of biodiversity conservation; however, as a taxonomist by profession and passion, he always advocated the significance of taxonomy. Wilson wrote "Descriptive taxonomy is not just a service agency for the rest of biology. Its product is far more than a stock inventory of Earth's biodiversity. Rather, given the extreme particularity of species and how little we know about them as a whole, taxonomy can justly be called the pioneering exploration of life on a little known planet. Among its cascade of derivative functions, taxonomy lays the foundations for the phylogenetic tree of life, it provides a requisite database for ecology and conservation science, and, not least, it makes accessible the vast and still largely unused benefits offered by biodiversity to humanity" [13]. Corrie Moreau, Wilson's PhD student and currently professor at Cornell University, states, "Dr. Edward O. Wilson's research was important in so many ways, but his taxonomic contributions are likely his most important. The discovery and description of new species is fundamental to all areas of biology and serve as the foundation for every discovery and theory in our field. Ed, as he was called by his closest colleagues and friends, described hundreds of new ant species and, along with Dr. Bert Hölldobler, really put ant research at the forefront of science. Even with over 14,000 species of ants already described, let's hope the world continues to value taxonomy because we have so many more species that are understudied and have not been formally named by scientists. Ed really helped the

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world see that the little things under their feet have an important role in every ecosystem".

Dubbed "the Darwin of modern times", credited with the discovery of 418 new species of ants and many species named in his honour, Wilson had an everlasting wish, "Anywhere I am in the world, I love it when the air is warm and moist, and heat bounces off the sunlit earth, and insects swarm in the air and alight on flowers and come in droves to lights at night, I remind myself that their species number in the hundreds or thousands. None to me is a bug. Each instead is a kind of insect, the legatee of an ancient history adapted to the natural world in its own special way. I wish I had a hundred lifetimes to study them all" [14].

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