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THE ROLE OF ABIOTIC STRESS IN IMMUNOLOGY

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Abstract. In the postgenomic era, interactions between organism and environment are central in disciplines such as epigenetics, medical physiology, and immunology. Particularly in the more "applied" medical felds, an emphasis lies on interactions of the organism with other organisms, that is, other living things. There is, however, a growing amount of research investigating the impact of abiotic triggers on the immune system. While the distinction between biota and abiota features heavily in other contexts, its status is not explicit within immunology. Do immunologists distinguish living from nonliving triggers? In this article, I will carve out whether and in which ways the biotic/abiotic distinction operates in immunology. I will look into responses to biotic and abiotic stressors in plant and invertebrate model species and ask how and why they are conceptually separated. I will trace the reasons by investigating the disciplinary situatedness of immune phenomena and the import of vertebrate immunology when conceptualizing immune responses in other model organisms. I will then investigate how the convergence of biotic and abiotic stress responses in plants and invertebrates adds to the recent philosophical programs advocating an ecological perspective on immune systems.

Keywords: Biotic/abiotic distinction, eco-immunolog, environment, invertebrate immunology, model organisms, philosophy of immunology, small RNAs

The distinction between biotic and abiotic stress is probably one of the least questioned dichotomies in physiological research. At the same time, it is one of the most ubiquitous, applicable to mammalian, invertebrate, plant, and prokaryote stress responses. The biotic–abiotic distinction divides things that exist into those that live and those that do not live. In doing so, it rests on an immediate intuition that a meaningful distinction can be made between, for example, my cat and my mat. For the study of stress responses, the biotic–abiotic distinction translates into the demarcation of the following groups of stressors: Viruses, bacteria, yeasts, fungi, or helminths are "biotic stressors." Heat shock, osmolarity, heavy metals, or radiation are "abiotic stressors." The separation of biotic and abiotic stressors is sometimes not entirely straightforward or undisputed.[1]

It is not the goal of this article, however, to assess the categories of "biota" and "abiota" in terms of necessary and sufcient conditions. The question, instead, is whether and to what extent the diferentiation is a guiding principle in immunology and what are the philosophical implications. One crucial philosophical consequence lies in the conceptualization of the environment. Recent developments in eco-immunology move away from viewing the immune system's primary task in providing "mechanisms of insularity" [2]but emphasize its role in "how the organism becomes an integrated constituent of alarge community" (2016). The question is, however, what is the place of abiota in this community? If immunology is extended to incorporate responses to abiotic triggers, how and where to draw the boundary of immune phenomena? How well do cognitive metaphors and agential thinking, omnipresent in immunological discourse, sit with responses to abiotic stimuli? Despite a general consensus that the immune system interacts with abiotic triggers, these questions still need to be addressed. In this article, by investigating the small RNA-based stress responses of an invertebrate and a plant model organism (MO), I will frst show how a particular version of the biotic/abiotic distinction is more or less tacitly assumed in

these MOs. I will then question the validity of the distinction, arguing that responses to biotic and abiotic stressors mechanistically converge. I will proceed and inquire about the philosophical consequences of this convergence. First, I will ask how the disciplinary situatedness of certain sets of phenomena, such as immune phenomena, influences the conceptual resources at work. I will argue that the role abiotic triggers play in vertebrate immunology infuences conceptualizing immune responses in invertebrates. Second, I will inquire how this situation bears on more prominent debates in immunology and its philosophy: How does the inclusion of responses to abiotic triggers infuence our notions of immunity? How do cognitive metaphors square with interactions of the immune system with abiotic triggers? And, how does a denaturalization of the biotic/abiotic distinction contribute to eco-immunological perspectives? In short, I will consecutively argue that the mechanistic convergence between small RNA responses to biota and abiota obtains; is not acknowledged in current invertebrate and plant immunology; but matters[4]. Small RNA Responses to Biotic and Abiotic Triggers in Invertebrates and Plants In this section, I will first introduce some basics about small RNA biology and then move on to discuss small RNA responses to biotic and abiotic stimuli in a plant and an invertebrate MO. Quite generally, small RNAs are noncoding RNAs studied for their regulatory roles in almost all known species. Studies on small RNA-related efects in the 1980s and 1990s culminated in identifying the phenomenon of "RNA interference" , referring to the fact that small RNAs interfere with, that is, change, gene expression. Small RNAs' primary mode of action is the complementary binding of target RNAs, although mismatches are sometimes tolerated depending on the particular class of small RNAs To ensure this targeting, small RNAs often rely on other efector proteins. Small RNAs are best known for targeting and sometimes destroying complementary messenger RNAs, inhibiting the synthesis of a specifc protein. Small RNAs are involved in several regulatory tasks, such as defense against selfsh genetic elements , metabolic regulation, and defense against viruses [5]. Several diferent small RNA species are defned based on diferent biochemical properties. Across MOs, however, tasks of particular species of small RNAs vary. Thus it is essential to point out before going into the details of small RNA responses in a particular MO that these are not general claims and cannot be extrapolated easily onto other model species or even transformed into general sentences. In almost all organisms that display small RNA-based gene regulatory circuits, small RNAs have been implicated as important regulators of stress responses to biotic and abiotic triggers. In plant and invertebrate immune systems, small RNA responses to viral infections are believed to be critical efectors of what is generally perceived as the "innate" immune system. In these scenarios, small RNAs, together with other immune efectors, guarantee resistance to these triggers by implementing gene regulatory changes that guarantee specifc resistance to the particular trigger. In the subsections to follow, I will focus on small RNA immune efector functions. Recent scholarship in plant immunology has, however, emphasized the importance of studying immune and abiotic signaling networks together but nevertheless treats abiotic responses as distinct from immune responses . Instead, these strands of research inquire about which nodes both signaling networks converge [6]. When biotic and abiotic stressors are considered together, research questions are raised in a way that asks for the efects of abiotic stressors on the immune system as in, for instance, increasing disease susceptibility, or how the plant fne-tunes immune responses in response to other environmental stimuli. Thus, plant immunologists consider the immune system "tunable" by abiotic stressors but only tunable with regards to pathogen resistance [7]. They observe "environmental modulation of plant immunity" and "roles for immune regulators in abiotic stress tolerance" That the immune system might provide immunity to the abiotic is not part of these considerations, which is also mirrored in linguistic choices, describing responses to abiota as "resistance" or "tolerance," but not "immunity." A somewhat striking fnding is that frequently, small RNAs are not even mentioned as immune efectors or only casually mentioned for their involvement in virus response. Instead, researchers focus on pattern-triggered and receptor-triggered immunity, processes that are somewhat similar to vertebrate innate immunity. Most of the time, small RNA-based immunity is discussed in separate articles and reviews that exclusively consider the contributions of small RNAs to immunity. In these reviews, only small RNA responses to biota are considered [7]. Even though there are several similarities of small RNAbased responses to biotic and abiotic stressors in invertebrates and plants, these similarities are not thematized in the immunological literature. Abiotic stress responses are not considered part of, but at most potential infuences on the immune response. Given this status , let me thus

formulate an argument why small RNA-based responses to biotic and abiotic stressors should be considered part of the immune response. Particularly in the plant immunology feld, researchers have observed a certain convergence of abiotic and biotic stress responses, meaning that efectors have been reported to be involved in both types of pathways [8]. With the small RNA example at hand, I shall, however, give the convergence argument more substance—not only are some efectors involved in both types of responses, but the small RNA-based system shows mechanistic convergence. I have asked whether and why a distinction between biota and abiota is operational in invertebrate and plant immunology. I have argued that a clash of representational spheres (between the dominant MO of immunology and the dominant MOs in "basic research" disciplines in which the phenomena were uncovered initially) that is governed by strong taxonomic polarities leads to the application of the soft biotic–abiotic divide—that non-corporeal abiotic triggers are not considered capable of priming immune memory towards them—in plant and invertebrate immunologyThis claim is more extensive since it does not only hold that certain entities might be part of biotic and abiotic stress response mechanisms, but that certain entities engage in the same or similar activities both in biotic and abiotic stress responses. I will provide a detailed mechanistic argument in what follows. Small RNA responses to abiotic and biotic triggers converge at the mechanistic level. Response to a particular stimulus leads to small RNA-caused gene regulatory changes and changes in the small RNA state guaranteeing specifc resistance to that stimulus. In conclusion, investigating any conceptual distinction brings to light the many ways that particularities of biological processes, disciplinary histories, applied versus basic research.

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