CellPress
REVIEWS

Scientific Life

Ecology and Evolution: Haeckel's Darwinian Paradigm

Elizabeth Watts,[1,3,*] Uwe Hoßfeld,[1,3] and Georgy S. Levit[2,4]

Ernst Haeckel coined the term ecology in the process of Darwinizing our understanding of nature. His concept of ecology was part of a theoretical system embracing development, evolution, and environment. We outline Haeckel's views on ecology as an evolutionary science and demonstrate their importance for current theoretical developments.

Darwin's Disciple

Prior to World War I, more people learnt about evolutionary theory from Ernst Haeckel's (1834–1919) publications than from any other source, including Darwin's own writing [1,2]. His great contribution to the dissemination of Darwin's ideas is often overshadowed by his promotion of a science-based universal worldview in opposition to traditional religions. His secular zeal enraged his religiously orthodox contemporaries and subjected him to subsequent creationist attacks in the 20th and 21st century [3]. Due to these accusations, Haeckel is often linked to alleged fraudulent illustrations of embryos and is therefore often seen as a divisive figure rather than a revolutionary scientist [2]. This image does not do justice to the true impact his work has had on science. He defined many of the most important terms and concepts used in biology today such as ontogeny, phylogeny, gastrulation, and ecology [4]. He also created the first 'trees of life' that acted as foundational concepts for future phylogenetic studies [5,6]. All of these conceptual innovations were published in his *General Morphology* [7], which he wrote as an exposition of Darwinian evolutionary theory in its entirety [8]. Incorporating Darwinian principles into all fields of the life sciences was arguably his most profound impact on the course of science history. To mark the 100th anniversary of Haeckel's death, we would like to outline his original views on ecology as an evolutionary science and to highlight the relevance of his holistic approach to biology on current theoretical developments.

Haeckel's Ecology

While it is well-known that Haeckel coined the term 'Oekologie' over 150 years ago [9], the true significance of this, and its effect on the course of scientific development, is often underestimated or entirely overlooked. Haeckel understood Darwin's fundamental message, namely, that the naturalist needed to consider the complex interplay between organisms and their environment in order to assess the 'advantage' of particular traits [1]. In this sense, Haeckel conceived 'Oekologie' together with 'Chorologie' (biogeography) as a subdiscipline of zoology and therefore of evolutionary theory, where the focus was on the study of organisms in relation to their organic and inorganic environment. As to the causal relationship between organisms and the environment, Haeckel as well as Darwin believed that the local environment could direct variation but that variation could also occur randomly. Both championed neo-Lamarckian mechanisms along with natural selection [7]. Haeckel's concept of ecology represented a symptomatic paradigm shift, as it was established within a conceptual system that integrated development, evolution, and environment [10]. Haeckel realized even during the onset of evolutionary research that it was only possible to truly comprehend any of these fields by first studying the interplay between them. His grasp of the intrinsic connection between ecology, evolution, and development is seen most clearly in the overview he offered in *General Morphology* (Figure 1).

The scheme entitled 'Zoology or Animal Science' reflected Haeckel's general subdivision of biology into morphology and physiology. Morphology was conceived as a general doctrine of forms (both external and internal) of living bodies and the laws that determine the relationship between these forms. The division of morphology from physiology in his diagram corresponds to his ideas of 'static' and 'dynamic' as he believed that every natural body is either in the state of equilibrium or in a state of perpetual change/movement. Morphology is thereby the study of stasis (i.e., a study of equilibriums), while physiology in Haeckel's mind was concerned with the study of changing, moving forces (i.e., a dynamic zoology). According to this concept, Haeckel's newly developed concepts of ontogeny and phylogeny were also nestled within the 'zoostatic' (this doctrine specifically applied to animals) portion of his conceptual overview, the 'zoodynamic' portion concentrated on physiology.

When we take a closer look at Haeckel's concept of physiology (Table 1) we again see how Haeckel focused on the interplay between development, ecology, and evolution as his idea of physiology concentrated on understanding the way organisms 'function', not only with regard to their internal environment (bodily processes) but also in connection with their external environment (biotic and abiotic). In Haeckel's mind, physiology was focused on investigating the causes (including physical-chemical causes) of 'Morphogenie', the occurrence of new morphological forms. In modern terms Haeckel speaks of the causes of evolution. For Haeckel, the environment played a major role in limiting organisms' existence, as all organisms are confined to living in a particular part of the world and the majority of species are confined to a very small part

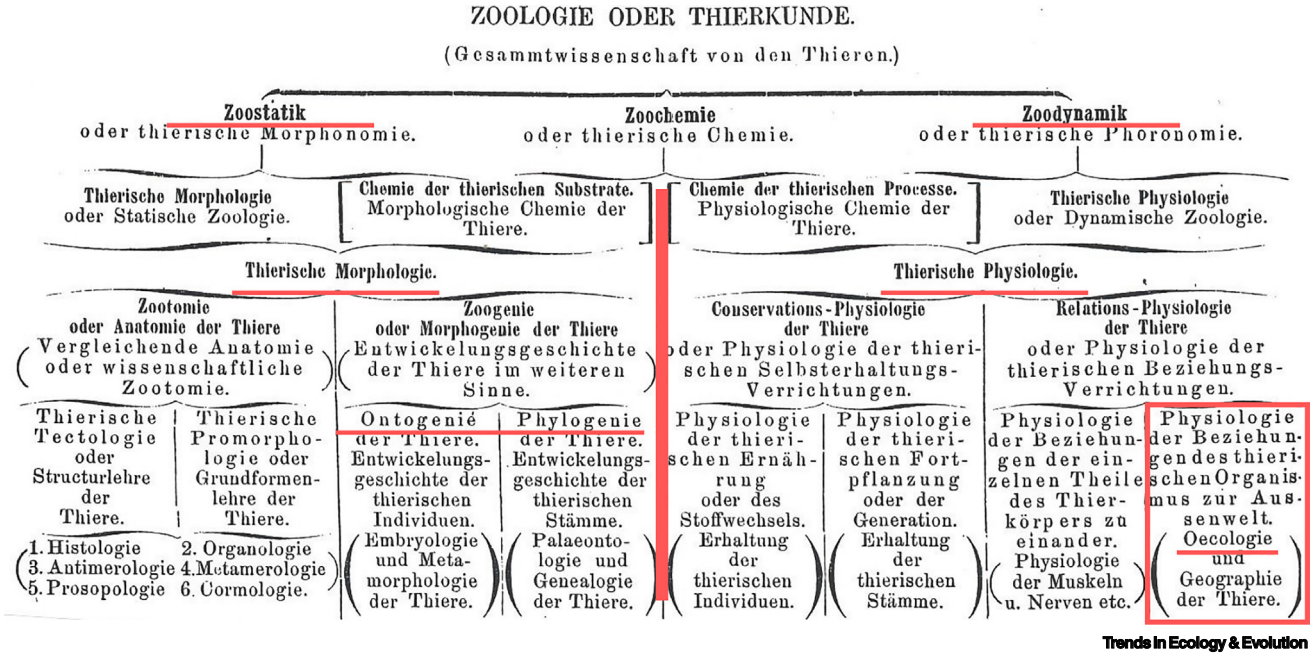

Figure 1. Haeckel's Overview 'Zoology and Animal Science'. It incorporates both the 'static' and 'dynamic' aspects of animal life, where 'static' is used to describe structures and forms (morphology), and 'dynamic' deals with movements, a state of change, or fluctuation [7]. (The red lines have been added to assist in the dissection of his conceptual paradigm as discussed in the text.)

of the Earth. This means that for each individual species there is a very small set of roles that they can fulfill within the 'Haushalt der Natur' (economy of nature). These limiting factors act as a cap that determines the maximum number of individuals that can coexist in a certain environment [7]. In this way, Haeckel grasped the most important concept of Darwin's theory, namely the idea that organisms are to be understood within a wide network of organic and inorganic factors [1] and it is out of this

Table 1. Comparison of Haeckel's Idea of Certain Terminology with Our Modern Understanding of the Same Terms

Term	Haeckel's understanding	Today's understanding
Physiology	Haeckel divided physiology into two parts: 'I. The physiology of conservation or self-preservation (a. nutrition, b. reproduction), II. The physiology of relations (a. physiology of the relation of parts of the organism to each other; ecology and geography of the organism or physiology of the relations with the external world)' ([7] Vol. 1, p. 237; cited from Jax and Schwarz [13]).	Focuses on the functions of living matter (such as organs, tissues, or cells), the physical and chemical phenomena involved, the organic processes and phenomena of an organism or any of its parts or of a particular bodily process. (based on Merriam-Webster)
Conservation	Self-preservation through nutrition and reproduction [7].	The intentional, careful preservation and protection of something, especially in terms of the planned management of natural resources. (based on Merriam-Webster)
Ecology	'By ecology we mean the whole science of the relations of the organism to its surrounding outside world, which we may consider in a broader sense to mean all 'conditions of existence'. These are partly of an organic nature and partly an inorganic nature' ([7] Vol. 2, p. 286; cited from Jax and Schwarz [13]).	The scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance [11].
	'By ecology, we mean the science of the economy, of the household of animal organisms. This has to study the entirety of relations of the animal both to its inorganic and its organic environments, in particular the benign and hostile relations with those plants and animals with which it comes directly into contact; or, to be concise, all those intricate interrelations which Darwin calls the struggle for existence' (Haeckel 1870, p. 365 [12]; cited from Jax and Schwarz [13]).	

idea of integrated understanding that modern ecology arose.

While the current idea of ecology focuses on how interactions between organisms and their environments affect their distribution (spatial concerns), Haeckel was much more focused on how these interactions affected an organism's evolutionary potential or were a result of their evolutionary past (temporal concerns). Even in the late 1800s, Haeckel's primary impulse was that development, ecology, and evolution needed to be contemplated as a unit in order to truly understand any of the individual components, and yet it was not until the early 21st century that the accuracy of this concept emerged through an increased understanding of the complex interplay between phenotypes and environmental conditions. Through current work in the field now known as eco–evo–devo (ecological evolutionary developmental biology), we now know, for instance, that phenotypes are dependent not only on the genome but also upon environmental cues, meaning that the environment acts not only as a selective agent but also in the production of phenotypes and thus plays a critical role in evolution [14].

Concluding Remarks

The idea of integrating research from developmental biology and ecology into evolutionary science, which gave rise to the field of eco–evo–devo [14], is Haeckelian in nature as it is fully in line with Haeckel's initial intention of fusing development, ecology, and evolution within a single conceptual space. Research in this field, for example, assimilates concepts such as developmental symbiosis and developmental plasticity into evolutionary theory [15]. While research in this field relies on modern discoveries, the concept behind this transdisciplinary approach is strikingly similar to Haeckel's research program in evolutionary biology, which was based on his understanding of nature as an interconnected and inherently dynamic whole, which can only be truly understood through a methodologically united system of sciences. The true dynamic nature of the living world has turned out to be even more intriguing than it was possible for him to imagine over 150 years ago. While Haeckel referred to all microscopic phenomena as 'chemical' processes, research in the field of eco–evo–devo has now opened our eyes to the immense role that this 'chemical' nature plays in our lives. The recognition of the intricate relationship between macrobiotic and microbiotic organisms has led experts to cease from perceiving of animals as individuals in the traditional anatomical sense and instead regard them as 'holobionts' or 'metaorganisms' that are home to numerous other (microbiotic) genetic lineages, and whose development and fitness is determined through the interactions with these [14]. While Haeckel could have never imagined what modern research in eco–evo–devo would divulge, he was a true visionary in his ability to recognize its core concept (i.e., that an understanding of both organismal development and ecology is necessary to truly comprehend evolutionary mechanisms).

[1]Research Group for Biology Education, Institute of Zoology and Evolutionary Research, Faculty of Biological Sciences, Friedrich-Schiller-University Jena, Am Steiger 3, Bienenhaus, 07743 Jena, Germany
[2]Institut für Biologie, Universität Kassel, Heinrich-Plett-Str. 40, 34109 Kassel, Germany
[3]Laboratory website: www.biodidaktik.uni-jena.de
[4]Laboratory website: http://www.uni-kassel.de/fb10/es/institute/biologie/fachgebiete/pflanzenphysiologie

*Correspondence:
elizabeth.watts@uni-jena.de (E. Watts).

https://doi.org/10.1016/j.tree.2019.04.003

References

1. Richards, R.J. (2008) *The Tragic Sense of Life: Ernst Haeckel and the Struggle over Evolutionary Thought*, University of Chicago Press
2. Richards, R.J. (2008) Haeckel's embryos: fraud not proven. *Biol. Philos.* 24, 147–154
3. Hossfeld, U. (2010) *Ernst Haeckel*, Orange Press
4. Egerton, F.N. (2012) *Roots of Ecology: Antiquity to Haeckel*, University of California Press
5. Hossfeld, U. *et al.* (2017) The first Darwinian phylogenetic tree of plants. *Trends Plant Sci.* 22, 99–102
6. Kutschera, U. (2016) Haeckel's 1866 tree of life and the origin of eukaryotes. *Nat. Microbiol.* 1, 16114
7. Haeckel, E. (1866) *Generelle Morphologie der Organismen, 2 Volumes: i. Allgemeine Anatomie der Organismen; ii: Allgemeine Entwickelungsgeschichte der Organismen*, Georg Reimer
8. Stauffer, R.C. (1957) Haeckel, Darwin, and Ecology. *Q. Rev. Biol.* 32, 138–144
9. Begon, M. (2017) Winning public arguments as ecologists: time for a new doctrine? *Trends Ecol. Evol.* 32, 394–396
10. Zigman, P.M. *et al*. Ernst Haeckels Biologie-Modernisierung und seine physiologisch-naturgeschichtliche „Oecologie" von 1866. *Ann. Hist. Phil. Biol.* (in press)
11. Townsend, C.R. *et al.* (2008) *Essentials of Ecology*. (3rd. edn.), Wiley-Blackwell
12. Haeckel, E. (1870) Über Entwicklungsgang und Aufgabe der Zoologie. *Jena. Z. Med. Naturwiss.* 5, 353–370
13. Schwarz, A. and Jax, K., eds (2011) *Ecology Revisited*, Springer
14. Gilbert, S.F. *et al.* (2015) Eco-evo-devo: developmental symbiosis and developmental plasticity as evolutionary agents. *Nat. Rev. Genet.* 16, 611–622
15. Gilbert, S.F. and Epel, D. (2008) *Ecological Developmental Biology: Integrating Epigenetics, Medicine and Evolution*, Sinauer Associates Inc.

Science & Society

Biodiversity Conservation Requires Management of Feral Domestic Animals

Cristián Bonacic [1,2,*], Rocío Almuna [1,3] and J. Tomás Ibarra [1,2,3,4]

The proliferation of feral domestic animals (FDAs) has been favored by human-induced landscape changes, a world population becoming increasingly urban, and by inappropriate management of domestic animals. Here, we describe the impact of FDAs and the opposing views in societies that affect the decision-making process and management actions. We provide general recommendations for the participatory management of this emerging threat to biodiversity and rural ecosystems.