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CLASSICS IN BIOLOGICAL THEORY

Revisiting Hans Böker's "Species Transformation Through Reconstruction: Reconstruction Through Active Reaction of Organisms" (1935)

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Abstract

Against the common historiographic narratives of evolutionary biology, the first decades of the 20th century were theoretically far richer than usually assumed. This especially refers to the hitherto neglected role that early theoretical biologists played in introducing visionary research perspectives and concepts before the institutionalization of the Modern Synthesis. Here, we present one of these scholars, the German theoretical biologist and ecomorphologist Hans Böker (1886–1939), by reviewing his 1935 paper "*Artumwandlung durch Umkonstruktion, Umkonstruktion durch aktives Reagieren der Organismen*" ("Species Transformation Through Reconstruction: Reconstruction Through Active Reaction of Organisms"), published in the inaugural volume of the journal *Acta Biotheoretica*. While largely forgotten today, this work represents a melting pot of ideas that adumbrate some of today's most lively debated empirical and conceptual topics in evolutionary biology: the active role of organisms as actors of their own evolution, environmental induction and phenotypic plasticity, genetic assimilation, as well as developmental bias. We discuss Böker's views on how species change through (what he calls) "*Umkonstruktion*," and how such reconstruction is exerted through active reactions of organisms to environmental perturbations. In addition, we outline the aims and wider context of his "biological comparative anatomy," including Boker's reprehensible political affiliation with the Nazi Party. Finally, we highlight some of the historical reasons for why Böker's views did not have a larger impact in evolutionary biology, but we also recount some of the direct and indirect legacies of his approach in research areas such as ecomorphology and (Eco)EvoDevo. Böker's paper is available as supplementary material in the online version of this article, as part of the journal's "Classics in Biological Theory" collection; the first translation of the paper into English, by Alexander Böhm and Jan Baedke, is also being published in this volume.

Keywords Hans Böker · Ecomorphology · Environment · EvoDevo · Genetic assimilation · Organism

Introduction

Currently, evolutionary biology is traversing an exciting period with a profusion of ideas ripe for debate and a deluge of empirical data amassed from different levels of biological organization. On the organismal level, sources of disputes include, among others, the extent of the bias developmental systems impose on the production of selectable variation, the role of environmental induction and phenotypic plasticity at the outset of evolutionary trajectories, the proper loci of evolutionary causation, broader views of inheritance beyond the gene, the causal agency of organisms as actors of their own evolution, and the multiplicity of processes by which the fit between individuals and environment is increased (see Sultan 2015; Edelaar and Bolnick 2019; Uller and Laland 2019; Baedke 2020; Levis and Pfennig 2020). At face value,

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this diversity of views might seem to be unparalleled in the history of evolutionism.

In recent years, historians have posed the metaphor of an "hourglass" to depict changes in studies on heredity and evolution from the second half of the 19th century up to the present-day (see Barahona et al. 2010; Levit and Hoßfeld 2011; Brandt and Müller-Wille 2016): at both ends we find bulbs encompassing a great variety of views held in the early 20th and 21st centuries, and a narrow neck representing a "constriction" of standpoints due to the institutional consolidation of genetics and the Modern Synthesis. The variety of evolutionary perspectives in the first decades of the 20th century is commonly only taken to include neo-Lamarckian or orthogenist alternatives to natural selection during the so-called "eclipse of Darwinism" (Bowler 1983). However, those decades were theoretically far richer than usually assumed. This especially refers to the hitherto neglected role that early theoretical biologists played in introducing and articulating visionary research perspectives and concepts that are currently regaining topicality in evolutionary biology (for overviews of this international movement, see Nicholson and Gawne 2015; Peterson 2016; Rieppel 2016; Esposito 2017; Baedke 2019).

Here, we introduce one of these scholars, the German theoretical biologist and ecomorphologist Hans Böker, by revisiting his 1935 article "*Artumwandlung durch Umkonstruktion, Umkonstruktion durch aktives Reagieren der Organismen*" ("Species Transformation Through Reconstruction: Reconstruction Through Active Reaction of Organisms"), published in the inaugural volume of the journal *Acta Biotheoretica* (Böker 1935a).[1] While largely forgotten today, this work represents a melting pot of ideas that adumbrate some of the most lively debated empirical and conceptual topics in contemporary evolutionary biology: the agency of organisms guiding their own development and evolution, environmental induction, phenotypic accommodation, and genetic assimilation, as well as facilitated variation and developmental bias. In this paper, we draw attention to the senses in which Böker's article is still relevant, especially in the context of evolutionary developmental biology (EvoDevo), as well as its importance to understanding the history of some protracted debates in the study of evolution.

After providing a brief biographical introduction to Böker, we describe his project to establish a "biological comparative anatomy" (*Vergleichenden biologische Anatomie*; better described as "ecomorphology") (second section). In that ambition, he pioneered the comparative study of vertebrates in the wild by linking morphological features with environmental factors. We then discuss Böker's views on how species change through (what he calls) "*Umkonstruktion*" (reconstruction) and how this process of reconstruction is exerted through the active reactions of organisms to severe environmental fluctuations (third section). After that, we highlight some of the historical reasons that explain why the impact of Böker's ideas on evolutionary biology was rather marginal (section four). This appraisal also deals with his reprehensible political affiliations with the Nazi Party. Finally, in the last section, we recount some of the direct and indirect legacies of his approach in research areas such as ecomorphology and (Eco)EvoDevo.

Biography and Works

Hans Böker (Fig. 1, left) was born in Mexico City on Nov. 14, 1886.[2] Two years later, his merchant family moved back to Germany. He later studied medicine in Freiburg, Kiel, and Berlin (1906–1911). Böker received his doctoral title with a work on the skull of the salmon (*Salmo salar*) in 1913 and habilitated with a study on the development of the trachea of sand lizards (*Lacerta agilis*) in 1917, both at the University of Freiburg. Throughout his career, he held positions at the Anatomical Institute in Freiburg (1912–1932), the University of Jena (1922–23, 1932–1938), and the University of Cologne (1938–1939). In Jena, he was the director of the Anatomical Institute. From 1934 onwards, he was a member of the National Socialist German Workers' Party (NSDAP) and the *Schutzstaffel* (SS; Hoßfeld 2015; see also the fourth section).

Shortly after World War I, Böker started to develop an innovative research program, which he called "comparative biological anatomy" (*Vergleichenden biologische Anatomie*; Böker 1935b) or "biological morphology" (*biologische Morphologie*; Böker 1924). It defended the idea that morphological research should not focus on reductionist analyses of anatomical parts of dead organisms in the lab, but on ecological studies that compare the development and evolution of living organisms' whole morphology in their natural habitats (Hoßfeld 2002; Hoßfeld and Olsson 2003). This holistic perspective initiated a research tradition of "ecomorphology" (Bock 1990), in which, according to Böker, ecology, ethology, and morphology should be united. Böker claimed that the evolution of new anatomical formations can occur in two ways: through a gradual transformation of

[1] Böker's paper in the original German is available as supplementary material in the online version of this article, as part of the journal's "Classics in Biological Theory" collection. The first complete English translation of the paper, by Alexander Böhm and Jan Baedke (Böker 2021), is also being published in this volume.

[2] For biographical details, see Hoßfeld (2002); Hoßfeld and Levit (2012); see also Nauck (1939) and Meyer-Abich (1941).

Fig. 1 Hans Böker at the German-Dominican Tropical Research Institute, Ciudad Trujillo (today Santo Domingo). Portrait of Böker (*left*) and his models of bird anatomy on the balcony of the Institute (*right*), 1937. Reproduced with permission of the State and University Library, Hamburg, Germany; collection NAMA, Da32

traits, or, more often, through fast, developmentally mediated change in organismic structures. The latter process is stimulated by the environment (as environmental changes push organisms out of their "morphological equilibrium state") but actively mediated and guided by the organism. The organism reconstructs individual anatomical features in functional consideration of its whole morphology as well as physical properties of the environment. We spell out Böker's theoretical standpoint in more detail in the next section.

This research was empirically fueled through various research excursions, among others, to Corsica, the Canary Islands, Amazonas (Brazil), Sahara, and the Dominican Republic. He published several books (e.g., Böker 1932a) and articles on the anatomical findings made during these trips (e.g. Böker 1927a, 1929a), especially on bird morphology (Böker 1927b, 1929b, 1930; Fig. 1, right). A central aim of these studies was not to find homologies, but to survey how similar ecological scenarios create evolutionary convergence across taxa. Besides these empirical investigations, he published on the history of biology (Böker 1936a, b) and on several topics of philosophy or theory of biology, like holism (Böker 1936a, b, 1937a, b) and mechanistic thinking (Böker 1935d), the relation between form and function (Böker 1937b), methodology in biology and medicine (Böker 1934a), and Lamarckism (Böker 1931, 1935c). His evolutionary framework tried to reconcile a (critically) reworked neo-Lamarckism with a Darwinian approach to natural selection. Here, Lamarckian direct induction was replaced by a strong emphasis on the active organism that incorporates and dynamically reacts to environmental change through reconstructing its whole anatomical constitution. Inheritance of acquired characteristics was replaced by a multigenerational selection process similar to that of phenotypic accommodation.

Böker developed his organism-centered theory in detail in *Einführung in die vergleichende biologische Anatomie der Wirbeltiere* (Introduction to the Comparative Biological Anatomy of Vertebrates; Böker 1935b, 1937a). Since Böker died suddenly on April 23, 1939, from an embolism, the third volume (on the anatomy of reproduction and reactions to the environment), which promised to be his most relevant evolutionary contribution, was never published. However, in 1935 he summarized the major evolutionary ideas of his work in a paper published in the first volume of the newly formed journal *Acta Biotheoretica*. The aim of this journal was to unite the international community in the young but rapidly growing field of theoretical biology (Reydon et al. 2005; Baedke 2019). One of the editors was Böker's closest professional friend, the theoretical biologist Adolf Meyer (later "Meyer-Abich") from the University of Hamburg. With contributions from John Scott Haldane, Karl Sapper, Edward Stuart Russell, Hans Driesch, Helmut Plessner, and Adolf Meyer, the first volume of *Acta Biotheoretica* included Hans Böker's (1935a) paper "Species Transformation Through Reconstruction: Reconstruction Through Active Reaction of Organisms." It provides an innovative attempt to develop a methodological synthesis between ecology, ethology, and morphology, and an evolutionary synthesis between Lamarckism and Darwinism. This was a synthesis quite different from the one attempted around the same time under the name of the Modern Evolutionary Synthesis (Huxley 1942).

Reconstructing "*Umkonstruktion*"

Böker (1935a) begins his article by presenting the causes of species transformation deemed to be prominent by most evolutionists of his time: mutation, orthogenesis, and hybridization. For Böker, mutation and orthogenesis expose organisms to the struggle for existence and selection, but both have considerable shortcomings. For instance, he countenances a limited evolutionary role for mutations on the basis that they "mainly concern exterior bodily features" (e.g., color or shapes of ectodermal formations), and lead to pathologies (1935a, pp. 17–18). He criticizes geneticists that advocated for single mutational changes (subsequently sieved by selection) as the mechanistic basis of evolution and, in particular, of "complex adjustment processes" of organismal bodies (see also Böker 1937b). This focus on the adjustment of bodily constitution is one of the most salient themes of Böker's theoretical work.

At that time, researchers explained these complex adjustment processes by appealing to Lamarckian inheritance of acquired characteristics, ruled out by some geneticists as a "logical impossibility," but not discarded entirely by others (e.g. Naegeli 1934), including Böker in previous articles (Böker 1931, 1935c). Böker countered that, "[t]he main objection against the inheritance of acquired characteristics states that these phenomena are not about changes in the genotype, but always only about the activation of potential dispositions of the existing tolerance range" (Böker 1935a, pp. 18–19). Amidst the heated exchanges of detractors and staunch adherents of neo-Lamarckism, Böker advanced his own views cautiously. Following Bertalanffy (1932), he noted that two different forms of "reasoning about the world" collide in Mendelism and Lamarckism: a static one and a dynamic. In that theoretical impasse, for Böker not resolvable on experimental grounds alone, he introduced the aim of his 1935 paper: "I seek to bridge the dichotomy by countering "exact" genetics as a theory of *passive mutation* with *comparative biological* morphology and its *theory of active reaction*" (1935a, p. 19; emphasis in original).

In his account there are two different types of biological change, namely one that impacts individual characteristics that are largely irrelevant for the life and adaptation of an organism, and another type of change that is caused by anatomical reconstructions that yield new adaptive potential. The first type of change is explained by the accumulation of genetic mutations that deal with the external appearance of organisms. As an example, Böker cites the carrion crow and the hooded crow, which are highly different on the outside, but share an underlying "anatomical structure" (1935a, p. 19). The process responsible for anatomical modifications is what he calls "*Umkonstruktion*" (see also Böker 1935b, 1936a, b). For Böker, anatomical reconstructions fall outside the purview of genetics altogether, a discordance that engendered tensions with morphological research.

To exemplify the idea of reconstruction and the role of active reactions of organisms as causes of evolution, Böker reviewed his research on the Neotropical crested chicken (*Opisthocomus cristatus*), also known as hoatzin, and the owl parrot or kakapo (*Strigops habroptilus*; see Böker 1929b). With his theoretical framework, he attempted to explain some convergent morphological changes in the evolutionary history of those two bird species. Böker maintained that both species experienced a profound perturbation in their bio-morphological equilibria due to changes in diet, specifically through a transition to eating very hard leaves. It is important to stress that, for Böker, whether this change in diet was actively chosen by the organisms or imposed by environmental shifts was in itself indifferent to the anatomical consequences it brought about. In response to this severe perturbation, the first active anatomical reaction was the formation of a large S-shaped crop.[3] That reaction led to a series of quantifiable anatomical changes in both birds with concomitant physiological consequences (1935a, pp. 21–22). According to Böker, the mismatch between crop and torso suggested a second perturbation for the mechanical reason that a large front weight disrupts flying ability, owing to an unfavorable weight distribution. A new series of organismic changes followed: the wing became larger to increase lifting capacity, the remiges lengthened, and the extra frontal weight was compensated by an elongated tail (1935a, p. 22). Drawing from embryological evidence, Böker argued that the third active reaction to the disturbed weight distribution was the migration of the crop to the front of the sternum (Fig. 2; see also embryonic illustrations in Böker 1929b). This, however, led to a constraint of the embryogenesis of the chest muscles which, at this point, the organism could only react to in limited ways. Böker then discussed the environmental conditions in which both species thrive, in addition to pointing out their interrelationships with changing anatomical constructions. In spite of these active morphological rearrangements, Böker argues, the kakapo can do without flying because it lives in mountainous terrains. In contrast, the hoatzin is a swamp forest dweller and cannot entirely give up flying, and thus finds itself in an unstable relationship with the environmental conditions that demand another active reaction to avoid perishing.

Levit et al. (2008) pointed out that Böker assumed that the organism is a "construction" built up from parts, although for him only the whole organism is confronted with its environment. As argued by his friend Meyer-Abich (1941), Böker's

[3] The hoatzin is the only extant bird species that feeds by fermenting leaves in its crop and esophagus. Its crop is folded into two interconnected chambers (Grajal 1995).

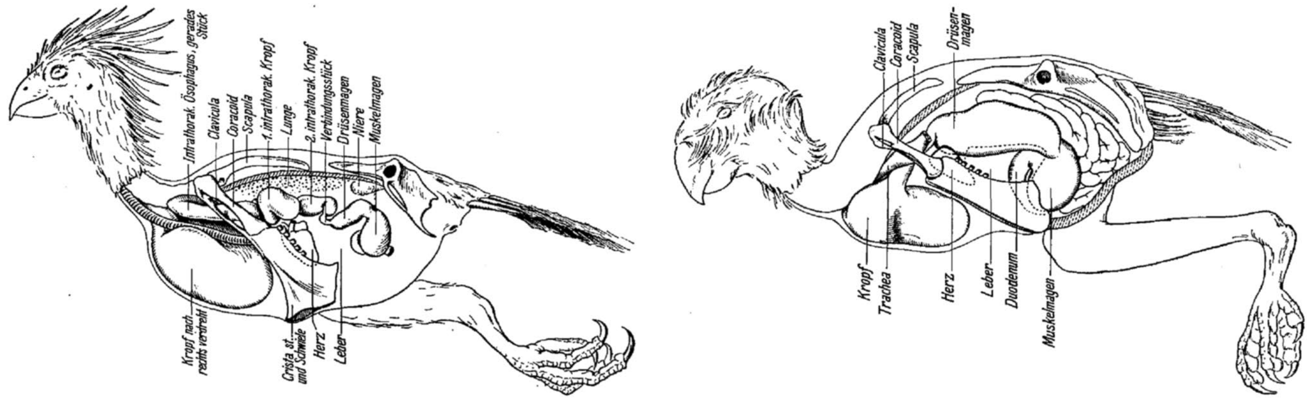

Fig. 2 Böker's anatomical drawings of *Opisthocomus cristatus* (*left*) and *Strigops habroptilus* (*right*). Both birds show an integration of their crops into the front of the sternum and less strong breast muscles. The anterior sternum is drastically reduced to make room for the crop, resulting in a reduction in the area available for flight-muscle attachment (Böker 1929b, pp. 168, 172)

stance was holistic (see also Böker 1931, 1932b): the organism, as a historical being, is understood as a whole that is in harmony with its parts and with the environment in which it thrives; whenever this bio-morphological equilibrium is disturbed by stimuli originating from the environment the organism must strive to regain it, otherwise it is at risk of expiring. Böker considered that if organisms cannot react to the challenges posed by the environment, the risk of extinction is extended to the species level. In contrast, in those instances where the organism actively reacts, adaptation proceeds through anatomical reconstruction of the whole organism or its parts, and new assemblages can be inherited. The intrinsic purposefulness of the organism striving to regain its bio-morphological equilibrium with the environment is nothing mystical nor related to conscious, volitional states, but it can be reinterpreted as the organism actively maintaining its own organization (see Nicholson 2013).

In the theorization of interlaced chains of changes initiated by the active reconstructions of organisms, we can see how Böker highlighted the relationships between morphology, physiology, and behavior. His holistic ideal is important for understanding what he extracted from the avian case study about convergent morphologies:

> It is completely impossible that the reactions could have been realized through passive random events, through mutation and selection. They were only possible through *holistic, i.e., meaningful and forward looking, active reaction*. […] Unsuited random mutations, which were deleted through selection so long until a new right coincidence happened, had to be avoided. Instead, in the sense of the holistic occurrence, internal meaningful structures, i.e., anatomic constructions, had to be maintained functional. No single genes were allowed to change, but complex combinations of genes as a whole had to be maintained in harmony! (Böker 1935a, p. 24; emphasis in original)

While different in style, Böker's assessment is reminiscent of current EvoDevo ideas about the nature and distribution of phenotypic variation, and how developing organisms are active mediators in the production of biased variation (see the fifth section). It is important to stress that, for Böker, the researcher can disentangle ontogeny from phylogeny (for the historical context of these discussions in the German-speaking world, see Rieppel 2016). The evolutionist aims to investigate the disorders of the bio-morphological equilibrium and the anatomical reactions to them in phylogenetic sequences. Drawing on Meyer-Abich (see Meyer 1926), Böker argued that phylogeny is much more than building phylogenetic trees and registering relations between "taxa" (a term Meyer-Abich coined), as it concerns a historical science that must attempt to investigate the causative factors behind the changes in organic form and the living conditions of organisms (Böker 1935a, p. 30).

We are now in a position to understand the crux of Böker's outlook on evolution and how he tried to bridge the gap between genetics and his ecomorphology:

> The process of active reaction happens during phylogeny. But the way in which this process is transferred to the germ plasma, so that the phylogenetic process occurs in ontogeny as hereditarily fixed process, is a technical problem. The question "How can a genetic change occur as a consequence of a vital change of behavior in an animal?" is a quite different one than "How is an anatomical construction reconstructed, if the vital expressions of an animal had to change?" The second question is a phylogenetic one, the first is a technical, hereditary-technical question. (Böker 1935a, pp. 24–25)

According to Böker, biologists need to draw a methodological distinction between phylogenetic studies of how species actively reconstruct themselves and questions about passive (genetic) inheritance of these *Umkonstruktionen.* He contended that genetic inheritance is a passive mechanism, which can, if necessary, be replaced by the active reaction of the organism to an urgent, severe environmental challenge (Böker 1935a, p. 25). In the latter case the organism affects the nature of variation and the speed with which it is produced and passed on. Böker argued that reconstructions unfold in phylogeny because active reactions to deep distortions do not appear in single individuals, but usually in all individuals of a species sharing one environment. In the case study of reconstructed bird morphology, this means that two ways of producing variation were at work. Random genetic variation produced passively in individuals could not counteract the urgent environmental challenges those birds faced. Thus, a second type of variation, directed and responsive to the nutritional stimuli, was needed to allow for rapid morphological change. Böker maintained that this latter variation did not appear randomly in individuals, here and there, but in many (if not all) members of a species exposed to the same environmental challenge and inherited in a Lamarckian-like pattern (with genetic mutations passively catching up). Hence, for Böker, reconstruction is a species-level process (although each organism faces the environmental challenge individually) and should be studied phylogenetically. As a consequence, it should be noted that the explicit organism-centeredness of Böker's evolutionary perspective is problematic, because the role of individuals is actually downplayed in evolution: he postulates that reconstruction occurs on the species level, whilst highlighting the role of the active constructing organism.

In his article, Böker touches the subject of which type of environmental influences are important to ignite the active reaction of the organism en route to species transformation via reconstruction. He grants that not every environmental factor that alters organisms will have intergenerational consequences by directly affecting inheritance. Those are examples of what, at the time, were called "*Dauermodifikationen*" (enduring modifications) by Woltereck (1931).[4] In these cases, according to Böker, after one or a few generations the environmental stimulus needs to be present anew for variation to be engendered (e.g., changes in head morphology in *Daphnia*). More interestingly, Böker highlights a second type of environmental influence that can eventually be fixed in the nuclear hereditary material: "Once we know in detail when an environmental influence takes the form of a perturbation of the bio-morphological equilibrium, […] then we can reveal the time needed to hereditarily fix such a transformation of species" (p. 27). Perturbations of this second kind beget sustained, active reactions of organisms, which ultimately lead to the genetic fixation of new *Umkonstruktionen* of species (for a discussion on the parallels with genetic assimilation, see the fifth section).

The previous discussion might suggest that, for Böker, the environment took a prominent role in evolution. This notwithstanding, he is very insistent in stating that the ultimate determinant of evolution is the active organism itself and not the environment – contrary to the stance that, for him, is instantiated in both Darwin's and Lamarck's theories. The production of variation is never directly determined by a specific environmental change, as the organism advances step-by-step towards the solution (in unexpected ways) by drawing on several developmental "options" (see the fifth section). For Böker, the environment not only is a reservoir of selective pressures or of inducing stimuli that modify phenotypes, but also the trigger of the active responses of organisms when perturbations cross the threshold of the bio-morphological equilibrium. It is worth quoting him extensively:

> It depends on the intensity and speed of perturbating influences, and on the degree of the organisms' ability and readiness to react. Every single time a change of species through reconstruction is an active, a holistic event, never a passive mechanistic one. A. Meyer […] describes this idea as follows: "Organisms are never only passive adaptations to the organic environment." […] The actual reorganization of organisms is always an *active act of creation* of the organisms themselves that matches their inner world [Innenwelt]. Both Darwinism and Lamarckism have ultimately failed because of their conflation of *active adaptive insertion* [Einpassung] with *passive adaption* [Anpassung]. Both are theories of milieus that attribute to the environment active, creative forces in the process of species transformation. (Böker 1935a, p. 28; emphasis in original)

Moreover, Böker emphatically tried to distance his theory of reconstruction from Lamarckism, claiming non-equivalence on the grounds that anatomical redesigns happen at the level of species in phylogeny (and does not only involve individual transformations).

[4] What nowadays biologists have rephrased as cases of "transgenerational plasticity" (see Bell and Hellmann 2019).

Böker recognized that there are additional processes through which species could change (e.g., mutation, orthogenesis), but he dismissed them as being of insubstantial evolutionary importance (Böker 1935a, p. 29). For instance, he claimed that orthogenesis merely leads to pathological conditions or dead-ends in evolution,[5] and mutations are said to only change species by altering indifferent characteristics, otherwise a larger perturbation would ensue and selection or an active organismal reaction would accordingly intervene. Thus, active reaction is, for Böker, the most important evolutionary causal process. Böker proclaims that this evolutionary perspective has a clear dynamic, processual character:

> The theory of active reaction […] is based on dynamic and biological thinking; it thinks in terms of processes, processes of phylogeny and function; it is based on genetic-constructive thinking [genetisch-konstruktivem Denken]. Reactions change anatomical constructions, these reconstructions gradually become fixed in the hereditary material, and, once they regain as a whole their bio-morphological equilibrium, remain constant until they are forced again to react to new perturbations of the bio-morphological equilibrium. (Böker 1935a, pp. 30–31)

Böker advocated for a more pluralistic evolutionary theory that builds on phylogeny (broadly construed, not merely focused on systematics) and that adds to the static theory of genetic mutations dynamic and processual explanations about how environmental change and morphological reconstructions go hand in hand in the history of species. He described this pluralistic framework by means of a metaphor of a nervous horse pulling a wagon. This horse is put on a leash by the rider, whereby the rider represents the organism and the horse the variation produced. The "rider" controls the susceptibility to danger (whenever there is an environmental perturbation of the bio-morphological equilibrium) by directing and constraining the reactions of the "horse" (i.e., switching from random to biased variation) in order to avoid unbridled rushes in cases of distress. In short, the organism directs and constrains the way variation is produced (and then inherited) in face of urgent environmental challenges. To use Böker's own words: "In the transformation of species active reaction precedes passive mutation and it gives mutations a meaning and aim" (Böker 1935a, p. 32).

[5] For Böker (1935a, p. 29), orthogenesis "describes a development that depends on inner factors, which forcibly continues in the same direction and that can even lead to very peculiar, extreme forms." As an example of this process he cites the disproportionate formation of certain beak shapes in birds and antlers in some deers. According to Böker, orthogenesis entails "a certain bias in the ability to react," and this limitation amounts to the pathological character of the process (see also additional examples of tail size in parrots in Böker 1932a).

Reception of Böker's Organism-Centered Approach

Böker's approach had its most direct impact on Hamburg-based theoretical biologist Adolf Meyer-Abich (see Amidon 2008). The idea of reconstruction was expanded by Meyer-Abich by arguing that individuals not only construct themselves in interaction with their environment, but they also construct each other in symbiotic ways, as what he called "holobionts." His theory of holobiosis through reconstruction anticipated many elements of later theories of endosymbiosis and today's discussions on host-microbiota coevolution (see Baedke et al. 2020). After Böker's death, Meyer-Abich published an edition dedicated to his *Umkonstruktion* theory in order to make it more public (see Meyer-Abich 1941). However, this plan largely failed, and Böker's direct impact on the biological sciences remained rather limited (but see below).

This was due to several factors, from theoretical to social ones. Hoßfeld and Levit (2012) argue that his theory was not in line with, and partly ran against, some mainstream theoretical ideas in German evolutionary biology (see also Battran 2016). This was only in part due to Böker's Lamarckian ideas. The acceptance of neo-Lamarckian views during this time was complex (see Harwood 1993; Levit et al. 2008). On the one hand, Germany had a long tradition of conceptualizing organismic change in terms of processes "striving for a goal (*Zielstrebigkeit*) and following an inner necessity (*innere Notwendigkeit*) latent in the organism" (Hutton 2005, p. 191; emphasis in original). On the other hand, during the National Socialist (NS) period, ideas related to Lamarckism were increasingly associated with Jewish thinkers, as under this theoretical framework body transformations were considered possible during a lifetime.[6] This plasticity implied that racial differences were not fixed, which was against the dominant ideology of the NS Party (Hutton 2005, pp. 191–192).

A more severe problem was Böker's emphasis on holism. We should stress that although holistic perspectives bolstered to some degree NS ideology, the relationship between them and the Nazi regime was never straightforward (see Harrington 1996). Particularly, holistic views were not favored in many German academic circles of the time, including many biologists in Jena, and tended to be considered anti-Darwinian (Hoßfeld 2002; for a wider discussion, see Rieppel 2016). Even though Böker's holism was shared by Nazi supporters such as Karl Kötschau, Ernst Lehmann, Adolf Meyer-Abich, and Wilhem Troll, this trend towards holism was particularly attacked by "technocratically

[6] But see, e.g., Meloni (2016) on Lamarckian defenders of National Socialism.

oriented geneticists and racial anthropologists" (Hutton 2005, p. 179), and especially by Jena-based race hygienist Karl Astel (see Harrington 1996, pp. 195–198). Astel had a strong influence on Nazi eugenics and university research programs (Deichman 1996, p. 258). His presence in the university environment in Jena was likely an important factor in Böker's decision to take up a position at the Anatomical Institute at the University of Cologne in 1938. In 1936, Astel was instrumental in preventing the appointment of Meyer-Abich, Böker's scientific friend and holist, to a professorship in theoretical biology. A heated debate (labeled "*Akademiestreit*") emerged from this failed appointment, in which besides Böker, Meyer-Abich, Kötschau, and Astel, NSDAP officials were also involved. A statement from Böker in 1936 describes this debate: "Today, in the context of the frequent opposition against the theory of wholeness, […] an academic dispute emerges again, in which biological thinking is pitted against mechanistic thinking, the theory of the ability of active reactions against passive mutations, and the claim for synthesis against the claim for 'exact' analysis" (Böker 1936a, p. 134).

Despite his negative experiences with NS ideology in Jena, Böker actively tried at several points to sell his holistic views and his theory of reconstruction to the Nazi regime. In 1934 Böker joined the NSDAP and became a supporting member of the SS and other NS organizations. He participated in the advisory board of the *Zeitschrift für Rassenkunde* (Journal for Racial Science, edited by Freiherr von Eickstedt) and published two papers in its first volumes (Böker 1935c, d) as well as in other NS publication organs. While his 1935 *Acta Biotheoretica* paper does not include ideological statements, in the following years Böker was increasingly willing to link his theory of reconstruction with NS ideology, including race theory.[7] In 1937 he stated:

> Organisms are not passive dice, who have to put up with how chance plays with them, but they are active beings, which struggle for their life's work. This is an insight, which likely is more natural for us Germans compared to the plain mechanistic theory of mutation and selection, since we are also actively militant and not passively enduring. "Who wants to live has to fight, and who does not want to fight in this world of eternal struggle, does not deserve life!" Adolf Hitler. (Böker 1937a, p. VI; quoted in Hoßfeld 2002, p. 160)

[7] In his 1935 paper, Böker, however, cites (but also critically discusses) the views of geneticist Alfred Kühn on mutations and environmentally induced variations, which were published in the book *Erbkunde, Rassenpflege, Bevölkerungspolitik* (Heredity, racial welfare, population policy) (1935) by Kühn, pathologist and race theorist Martin Staemmler, and demographer and eugenicist Friedrich Burgdörfer.

Such commitment to NS ideology conflicted with his theoretical approach to some degree. His theory of reconstruction cannot easily be linked with Social Darwinism (as it was presented in opposition to strict selectionist views). In his attempt to link his ideas to Nazi race ideology, he excluded humans from his view of evolution through reconstruction (Böker 1934b). Instead, he drew on popular ideas of race theoretician Hans F.K. Günther to argue that human races are less plastic and susceptible to environmentally induced changes (e.g., in contrast to the races in the animal kingdom), thus making transition between human races less likely (see Battran 2016). This means that his view on human races followed the same direction as the overarching project of the NSDAP.[8] Besides these theoretical alignments to NS ideology, Böker worked in institutions directly funded by the regime, like the German-Dominican Tropical Research Institute near Ciudad Trujillo (Fig. 1, right). Notwithstanding his efforts and compliance with the Nazi regime, his theoretical (especially holistic) views remained suspicious for some officials, including the Reich Ministry of Science, Education, and Culture. Thus, despite a number of endeavors to link his biological work with NS ideology, these attempts largely failed.

We acknowledge that Böker's political ideologies and his involvement with NS institutions are more than condemnable. However, we believe that his theoretical contributions should not be overshadowed by this political context or merely reduced to it. In particular, his reconstruction theory was clearly motivated by many research trips conducted in the 1920s (leading, e.g., to Böker 1929b, 1931, 1932b). In addition, his underlying ecomorphological research framework can be traced back to his habilitation in 1917, long before the Nazi party came into power.

From an international perspective, Böker was not able to introduce his work to the emerging population genetic research community and could not partake in the increasing institutionalization of the Modern Synthesis (Hoßfeld and Levit 2012). Despite this, it is possible to

[8] This indicates that Böker was taking part in the ongoing conversation on NS ideology, albeit not in a central position. He was immersed in the same discussions pertaining to the biological sciences (e.g., on the concept of "race") as others of his Nazi-sympathetic peers. Recent historical scholarship has shown that different interpretations of ideological core elements coexisted and competed inside the NSDAP, in what has been referred to as the "polycentrism of Nazi ideology" (see Steizinger 2019). As a consequence of this pluralism, scholars could hold different biological views of human races that could be integrated within the same ideological framework. Böker, from the mid-1930s onwards, actively framed some of his ideas with the language and lens of the NS polycentric ideology. His dissent in some topics from mainstream theoreticians or the theoretical nuances he supported (e.g., on holism and Lamarckism) do not exclude him from being a collaborator (even if of secondary importance) in NS ideology.

find references to Böker's work in central texts in the field, such as Ernst Mayr's *Systematics and the Origin of Species*. In a subsection called "The principle of harmonious organic reconstruction," Mayr (1942, p. 295) qualifies Böker's objections to the genetic-selectionist view as "particularly impressive." Besides Mayr, especially Bernhard Rensch's reception of Böker was very positive (Rensch 1947; see Levit et al. 2008). Of the "architects" of the Modern Synthesis, Rensch was possibly the closest to Böker's approach. Rensch was a former advocate of Lamarckism and was deeply interested in organism-environment interactions. He tried to give Böker's theory of reconstruction a more Darwinian reading.

At the early age of 52, Böker died in 1939 from an embolism during an appendix operation in Cologne, only a few months before the beginning of World War II, which led to years of interrupted international communication in the biosciences (Bock 1990, p. 258). This, plus the abrupt decline of German holistic biology after 1945, surely influenced the immediate national and international reception of Böker's biological comparative anatomy.

From Böker to EvoDevo

At first glance it seems that Böker's ecomorphology was largely forgotten after World War II. In fact, until today, his 1935 paper in *Acta Biotheoretica* – one of the few journals he published in with an international profile – has been cited only four times in the same journal, and a few times in other biological periodicals. This lack of impact is not least due to the fact that Böker's approach failed to provide a clear mechanistic understanding of how organisms act as mediators of morphological reconstructions, how exactly genes take over variation produced by the phenotype, and how precisely the organism-environment "harmony" should be understood. However, each of these theoretical points anticipated by him were empirically tested and clarified by other researchers in the following years.

This includes, first, research on genetic assimilation. For example, Conrad Hal Waddington (1942, 1953, 1956) experimentally investigated in *Drosophila* how the genetic capability to respond to strong and disturbing environmental influences during development is crucial for fixing developmental traits in the genome. In this process, an environmentally induced phenotypic character is, through selection and recombination, taken over by the genotype, so that finally the initial stimulus is no longer necessary to develop the new phenotype. In other words, the novel induced phenotype is progressively in more direct control by the genes. Nevertheless, and against Böker's Lamarckian reading of the process, "[t]here is nothing Lamarckian about genetic assimilation" (Hall 1992, p. 118). According to Waddington, genetic assimilation fully rests upon neo-Darwinian, Mendelian genetics. In contrast to Waddington, Böker was not searching for a mechanism of transgenerational fixation of traits on the level of genes (i.e., preexisting, yet hidden cryptic genetic variation), but on the level of the organism that guides and directs the origin of novel morphological traits (with genetic variation catching up passively). The process described by Waddington, leading to the emergence and gradual genetic fixing of new traits (induced through radical environmental changes) has been given a molecular explanation through work on the protein chaperone Hsp90 (Rutherford and Lindquist 1998; for discussion, see Millstein 2007).

Second, Böker's idea of the internal drive of organisms to maintain the functional harmony of their whole morphology became reinterpreted in the framework of nonequilibrium thermodynamics (Schrödinger 1944; see Nicholson 2018; Baedke 2019).[9] Here the active organism maintains its internal organization in a way that machines are not able to. Some authors have asserted that Böker's approach leads to speculative "just-so stories" about how certain morphological features were adaptive responses to radical environmental changes (Hoßfeld 2002; Hoßfeld and Levit 2012). While there surely is a danger to this approach, Böker nevertheless was able to use this framework in a methodologically fruitful manner to collect evidence that supported his narratives of reconstruction (a prime example is the comprehensive avian case study discussed above).

Third, evolutionary narratives focusing on environmental (especially nutritional) changes and morphological responses, pioneered by Böker, are still (or again) present in evolutionary biology. For example, interdisciplinary investigations have shown that transitions in dietary and behavioral practices since the Neolithic period have led to changes in the human bite configuration, which biomechanically constrained the vocal system and thus enabled the origin of labiodental sounds (Blasi et al. 2019). In another study, environmental challenges (chiefly nutritional) associated with urban settings have rapidly evoked active morphological reactions in foxes that have begun "domesticating themselves" (e.g. shorter snouts to ease the transition to snuffling for discarded food in bin bags), and these changes, according to the authors, cannot be accounted for by random mutations, but due to the action of developmental biases in skull morphology (Parsons et al. 2020). Concerning birds, Böker's favorite model of study, new investigations of adaptive phenotypic plasticity in response to novel and ancestral environmental conditions are being pursued (e.g. Ho et al. 2020). As a possible mechanistic basis of plastic responses

[9] This also includes the harmony of systems of genes and their interactions, what today we would call gene regulatory networks (see Böker 1935a, p. 24).

to serious environmental challenges, researchers have also pointed to microorganisms as a source of rapid genetic variability for their multicellular hosts (Elgart and Soen 2018). These could trigger plastic developmental changes at the level of the host, which enhance the match between the phenotype of the "holobiont" and its surroundings, and might be transmitted to the next generation(s) due to diverse bacterial-mediated modes of transgenerational inheritance.

Fourth, constructionist and saltationist views on the mode and tempo of evolution, not only defended by Böker but also by many authors of the time, became influential and widely discussed, albeit strongly contested in evolutionary biology. This includes Böker's claim that macroevolutionary change cannot occur through small, additive mutations. Goldschmidt (1940) develops a quite similar idea. He argues that "the change from species to species is not a change involving more and more additional atomistic changes, but a complete change of the primary pattern or reaction system into a new one, which afterwards may again produce intraspecific variation by micromutation" (Goldschmidt 1940, p. 206). Goldschmidt's stance on saltationist evolution, however, is, in contrast to Böker's outlook, not primarily driven by organismal reactions but by the creative potential for variation stored in the genome. Furthermore, for Böker (1935a) the pace of evolution is variable: only when the organism "comes to the fore" to contend with changing environmental conditions can the evolutionary process be accelerated, otherwise slow, gradual mutations account for transgenerational changes.

Fifth, in recent years, a conceptual framework on organism-environment interaction that somewhat resembles Böker's account has been increasingly used as a fruitful starting point for a new "organism-centered perspective" on evolution (Laland et al. 2015; see also Diogo 2017). It studies how organismic development, together with environmental cues, affects the origin of variation and thus evolutionary trajectories. This approach accentuates the centrality of the organism, rather than genes or populations, for explaining evolutionary processes, and the importance of constructive development. This organism-centered approach argues for reconsidering the capability of nongenetic, developmental variation to bias and guide evolutionary change. In line with Böker's views, Mary Jane West-Eberhard (2003) claims that genes are probably more often followers in evolution than leaders. Instead, it is the complex, environmentally responsive system of the developing organism that takes the lead. In a nonrandom, biased manner, new phenotypes are introduced in populations and are subsequently stabilized by genes. This view is currently described as the "phenotype-first view" or "genes-as-followers view" of evolution. Laland (2017) argues, similarly to Böker's leash metaphor, that genes do not effortlessly hold phenotypes (or even culture) on a leash (as asserted by Wilson 1978, p. 167), but instead, that organismal, developmental phenomena (multiple leashed dogs in this case) lead the way for genes (a struggling dog walker) in evolution.

This picture envisioned by Böker has become influential, especially in the field of ecomorphology, and later in evolutionary developmental biology (EvoDevo; see, e.g., Callebaut et al. 2007; Diogo 2017). How did this happen despite Böker's low direct impact on his peers? Starting in the 1950s, a new movement of evolutionary morphologists and ecological morphologists developed ideas quite similar to those of Böker (van der Klaauw 1948, 1951; Bartholomew 1958; Davis 1960; Bock and von Wahlert 1965; see also Bock 1990).[10] The Dutch zoologist and theoretical biologist Cornelis Jakob van der Klaauw, editor-in-chief of *Acta Biotheoretica* from 1935 to 1958, was particularly heavily influenced by Böker's approach of biological comparative anatomy (see, e.g., van der Klaauw 1948). In addition, by drawing explicitly on Böker's theory, Bock and von Wahlert (1965, p. 270) stated that they wanted to continue his work on the intersection between ecology, morphology, and evolution: "We hope to establish an internally consistent framework of concepts pertaining to morphology, function, and environment, including the interconnections between them, and to use this framework as the basis for the elucidation of adaptation." While traces of Böker's theoretical work are absent in many citation analysis tools (e.g., Web of Science lists zero citations after 1945),[11] these post-war ecomorphological works had quite an impact, especially in recent years (e.g., Bock and von Wahlert 1965 has been cited 384 times; see Web of Science). In fact, this stance on ecologically informed evolutionary morphology later became significant for the emergence of ecological evolutionary developmental biology (EcoEvoDevo).

There are several interesting similarities between Böker's views and current debates in EvoDevo. Among others, this concerns developmentalist ideas about the origin and distribution of phenotypic variation, especially discussions regarding "facilitated variation" (Gerhart and Kirschner 2007) and "developmental bias" (Arthur 2004). It is contended that phenotypic variation available for natural selection is not distributed isotropically through random genetic changes, on account of certain evolutionary changes that were favored by specific ontogenetic trajectories, while others remained inaccessible. The history, dynamics, and organizational properties of developmental systems allow

[10] For a broader overview of the impact of morphological-constructivist approaches on 20th-century evolutionary biology, see Tamborini (2020).

[11] In contrast, there are some citations of his descriptive work (e.g., on bird morphology and the locomotor behavior of lizards) after the end of WWII (see, e.g., the database of the Biodiversity Heritage Library).

certain variants to arise more readily than others (see Uller et al. 2018), and this might be related to the "inherency" of their material constitutions (Newman 2017). For Böker, during chains of environmental distortions and active reactions, the organism has to increase the likelihood of certain variations arising to solve "equilibrium problems," but this usually entails unexpected morphological and physiological consequences as well as trade-offs, as we saw from the example of the hoatzin and the kakapo. In his view, the variation needed by the organism is not produced directly, seamlessly, nor consciously. In addition, the production of variation is never determined by a specific environmental change. Instead, the organism approaches a solution step-by-step and reacts to environmental distortions by drawing from several developmental "options." A modern reinterpretation of this view states: "The concept of developmental bias captures the observation that perturbation (e.g., mutation, environmental change) to biological systems will tend to produce some variants more readily, or with higher probability than others" (Uller et al. 2018, p. 489). Böker would add to this picture that each perturbation-induced modification can subsequently bias variation in the interrelated parts of the organism in a long series of changes that dovetail to restore the bio-morphological equilibrium with the environment (e.g. the mismatch between the large S-shaped crop and torso resulted in a disturbed weight distribution in these birds, which biased the migration of the crop and ultimately affected flight ability).

Böker (1935a) should be understood as a representative stepping stone on the way to a more pluralist theory of evolution, similar in this sense to the one increasingly called for by a number of evolutionary biologists today (Laland et al. 2015; see also Newman 2013). While it failed to provide a clear and detailed mechanistic understanding of how organisms act as mediators of morphological reconstructions, Böker's approach was highly innovative and ahead of its time. Rather than qualifying as a "classic of biological theory" due to the history of its reception, his 1935 article represents a nucleus of various theoretical ideas (now part of "classical debates") that were in the air during that time in evolutionary biology, ecology, and morphology. In addition, it provides a glimpse into the diversity of debates about the organism in early theoretical biology.

At a time when the Modern Synthesis was in the making, Böker sought a different kind of synthesis with a stronger focus on the origin of variation. This synthesis was one between Darwinism and Lamarckism, between genetics and morphology, between lab and ecological field research, and between ontogenetic and phylogenetic approaches. In the center of this failed synthesis stood the organism. The organism holds genetic variation on a leash, rather than, as has become common to think from the second half of the 20th century onwards, genes holding the leash to phenotypic variation.

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