Biology & Philosophy (2022) 37:17
https://doi.org/10.1007/s10539-022-09848-z

Two kinds of historical explanation in Evolutionary Biology

Nina Kranke[1]

Received: 24 June 2021 / Accepted: 24 March 2022 / Published online: 9 May 2022
© The Author(s) 2022

Abstract
Historical explanations in evolutionary biology are commonly characterized as narrative explanations. Examples include explanations of the evolution of particular traits and explanations of macroevolutionary transitions. In this paper I present two case studies of explanations in accounts of pathogen evolution and host-pathogen coevolution, respectively, and argue that one of them is captured well by established accounts of time-sequenced narrative explanation. The other one differs from narrative explanations in important respects, even though it shares some characteristics with them as it is also a population-level historical explanation. I thus argue that the second case represents a different kind of explanation that I call *historical explanation of type phenomena*. The main difference between the two kinds of explanation is the conceptualization of the explanandum phenomena as particulars or type phenomena, respectively. Narrative explanations explain particulars but also deal with generalization, regularities and type phenomena. Historical explanations of type phenomena, on the other hand, explain multiply realizable phenomena but also deal with particulars. The two kinds of explanation complement each other because they explain different aspects of evolution.

Keywords Narrative explanation · Historical explanation · Evolutionary explanation · Experimental evolution · Phylogeography · Evolutionary biology

Introduction

Evolutionary biology as a historical science shares characteristics with other sciences like chemistry and physics but also with human history (Harrison and Hesketh

✉ Nina Kranke
nina.kranke@uni-muenster.de

[1] Department of Philosophy, University of Münster, Münster, Germany

2016; Kaiser and Plenge 2014). For example, historical explanations can be found in human history as well as in the historical sciences. Recently, the topic of narrative explanation in the sciences has been increasingly fleshed out by philosophers (e.g., Currie 2014; Beatty 2016; Morgan 2017; Carrier et al. 2021). In this paper I present two case studies of explanations in evolutionary biology that result from studies of pathogen evolution and host-pathogen coevolution, respectively. I show that the characteristics of one of the explanations can be captured by established accounts of narrative explanation. The other one, however, differs from narrative explanations in important respects. The main difference between the two kinds of explanation is the conceptualization of the explanandum phenomena as particulars or type phenomena, respectively. I thus argue that aside from narrative explanations, there is at least one other kind of historical explanation in evolutionary biology that I call *historical explanation of type phenomena*.

By comparing narrative explanations and historical explanations of type phenomena, I carve out the characteristics of the latter. The two kinds of historical explanation in evolutionary biology have in common that they include temporal sequences and are population-level explanations that deal with transgenerational processes. However, they also differ from each other as they result from different research activities. While narrative explanations are generated by reconstructing past evolution, historical explanations of type phenomena in evolutionary biology result from studying known evolutionary pathways (e.g., through laboratory experimental evolution). Both explanations complement each other because they explain different aspects of evolution. Narrative explanations explain how and why biological populations came to be as they are by providing a temporal sequence of events that has led to their current state. Thus, one of the central activities of narrative reasoning in evolutionary biology is reconstructing an evolutionary pathway through ordering of relevant materials. Historical explanations of type phenomena, however, are not constructed through ordering, but through constructing and/or observing a temporal sequence that shows how a phenomenon arises in the processes of evolution. When historical explanations of type phenomena are generated, the temporal sequence is known and to a certain extent manipulated by the experimenter (e.g., when populations are exposed to novel environments). Also, historical explanations of type phenomena cover shorter time spans and are more fine-grained than narrative explanations in evolutionary biology. The most important difference, however, is that narrative explanations explain particulars but also deal with type phenomena, generalization and regularities while historical explanations of type phenomena explain multiply realizable phenomena, but also deal with particulars.

Time-sequenced narrative explanations

While early discussions of narrative explanation mostly revolve around explanations in accounts of human history (e.g., Danto 1962; White 1963), it is now recognized that narrative explanations also play an important role in the historical (natural) sciences (e.g., paleontology, evolutionary biology, geology; Kaiser and Plenge 2014; see also Hull 1975; O'Hara 1988, 1992; Beatty 2017; Roth 2017, 47–50; Ereshefsky

and Turner 2020; Huss forthc.; Hopkins forthc.; Carrier et al. 2021). In this section I discuss the central characteristics of time-sequenced narrative explanations (temporal narratives) in the historical sciences.[1]

Narrative reasoning usually starts with a puzzling phenomenon and the question how and why things came to be as they are (Little 2010, 29; Roth 2017, 44). In the historical sciences, the answer to this question references a temporal series that includes events that happened at earlier points in time (see Little 2010, 29; Martin 1968, 72f; Danto 1968, 201ff; Beatty 2017; Ereshefsky and Turner 2020). In other words, to explain the phenomenon of interest "we need a *backstory* that rewinds time to some event in the more distant past, and then takes us forward through events" (Beatty forthc., emphasis original). In time-sequenced narrative explanations, a sequence of intermediate states bridges an initial state and an observed situation which makes earlier and later stages comparable (Carrier et al. 2021, 14). One way of reconstructing the past is to look for traces (Cleland 2002; Currie 2018, 56) or clues (Ginzburg 1979) and infer past events from this evidence. Imagine, for example, that you come home from work to discover that your living room window is broken. You find pieces of glass and a football on your living room floor. You have not witnessed the actual event, the shattering of the window, but you will probably infer from the traces that the football caused the shattering of the window (see Cleland 2002, 487). This type of trace-based reasoning can be compared with detective work where the investigator tries to reconstruct the crime based on the clues that they find (Cleland 2002, 490; Ginzburg 1979, 276; Haines forthc.).

Another important feature of narrative explanations is that they can only be known retrospectively (Roth 2017; Danto 1962; Martin 1968, 74; Ereshefsky and Turner 2020). One needs to know how the story ends to be able to identify its beginning and unfolding. Danto (1962) has coined the concept of *narrative sentences* to express this aspect. Narrative sentences "give descriptions of events under which the events could not have been witnessed, since they make essential reference to events later in time than the events they are about" (Danto 1985, xii). Examples for narrative sentences are "The Thirty Years War began in 1618" (Danto 1962, 155) and "*a* is an ancestor of *b*" (Griesemer 1996, 66). Although the concept of *narrative sentences* is helpful to express the significance of retrospection in narrative reasoning, it is important to note that not all narrative explanations necessarily contain explicitly narrative sentences. Andrew Hopkins (forthc.), for example, argues that although explanations or interpretations in geology are narrative in character, narrative sentences and statements are rare in some geology papers and typically appear in abstracts or conclusions. However, he identifies many "(nominally) descriptive sentences laden with various cues which contain the implicit, underlying narrative of geological processes" and argues that a trained geologist automatically picks up these cues and "makes a range of default assumptions which are translated into causally connected sequences" (Hopkins forthc.).

[1] Morgan (2017, forthc.) and Carrier et al. (2021) argue that not all narratives are temporal. Carrier et al. (2021) distinguish between "narratives in the temporal sense" and "narratives in the coherentist sense". In Morgan's (2017) account of narrative ordering, time ordering is only one of several types of narrative ordering. In this paper, however, I deal with explanations in evolutionary biology and thus focus on "narratives in the temporal sense".

John Beatty (2016) draws attention to the role of contingency in historical explanations. He argues that narrative explanations account for contingent outcomes and distinguishes between contingency upon prior events and contingency *per se*. An event is contingent *per se* if it was "not bound to occur; it was possible, but there were other possibilities; it was a matter of chance" (Beatty 2016, 36). If an event depended on the occurrence of an event that happened earlier in time, it is contingent upon that event (Beatty 2016, 36). The events that are included in the temporal series of a narrative explanation have consequences for or make a difference to the outcome (Beatty 2017, forthc.). These difference-making events or "turning points" are contingent *per se* and subsequent events are contingent upon them (Beatty 2016, 36).

Through time-sequenced narrative explanations we learn how something, or someone has changed in the course of time and which steps have occurred that brought about the new situation. They are coherent, unified accounts of an entity's development in time (Roth 2017, 45; White 1963, 4; Ereshefsky and Turner 2020). Morton White (1963, 4) uses the concept of *central subject* to refer to the entity around which the narrative[2] is woven (see also Hull 1975; Ereshefsky and Turner 2020; Currie 2014). A central subject as the protagonist in narrative explanations can be a person, but the concept also applies to other entities like states (e.g., Unites States of America), species, earthquakes or lineages of traits (White 1963, 5; Hull 1975, 262; Ereshefsky and Turner 2020; Hajek forthc.). Mary Morgan (2017) also discusses coherence of narrative explanations and emphasizes the activity of ordering.[3] Building on Louis Mink's configurationalist account, she argues that narrative reasoning involves not just putting materials in order but also showing how they are connected or fit together (e.g., through causes, processes of change) (Morgan 2017).

Several philosophers of science argue that narrative explanations explain particulars (e.g., the origin of a particular revolution or trait) (Gardiner 1961, 82; Cleland 2002, 480; Tucker 2014, 349; Currie 2014, 1165; Roth 2017). It would be misleading, however, to say that narrative reasoning is only concerned with particulars. In fact, there are different ways in which narrative reasoning deals with type-phenomena, generalization, and regularities (see Morgan 2017, 87). Virtually all accounts of human history depend on concepts (e.g., revolution, monarchy) that frame particular events (e.g., the French Revolution) as instances of types of events. The use of these concepts indicates that instances of this type of event (e.g., the French Revolution, the Haitian Revolution) share common characteristics which makes them comparable to a certain extent. A different example of framing the unique history of a particular entity as an instance of something more general can be found in Steven Shapin's (2012) account of the Ivory Tower as a figure of speech. He gives a narrative explanation of "how and why the notion of the Ivory Tower became part of twentieth- and twenty-first century cultural vocabularies" (Shapin 2012, 1). At the end of his paper,

[2] In this paper I use the term *narrative* to refer to explanatory time-sequenced narratives that have the characteristics discussed in this section. A narrative in this context is not just any story that scientists tell themselves and others to make sense of what they are doing.

[3] Morgan (2017, forthc.) has a broad understanding of *narrative ordering* where temporal ordering is a subset of narrative ordering. However, she argues that "time-sequenced, narrative representations are found most likely in the historical sciences - natural and human/social - for these deal in matters of time *and* where time-ordering really matters" (Morgan forthc., emphasis original).

he situates his discussion in a broader context and argues that Ivory Tower talk "is a modern instantiation of the ancient religious and secular debate over the active and contemplative lives" (Shapin 2012, 26). Similarly, the global stock market crash of 2008 can be explained as an example of a familiar pattern of economic behavior (Glennan 2010, 262-3). In comparative studies, historians explicitly compare different historical episodes to draw general conclusions or infer causal connections. In his well-known book "The Rise and Fall of the Great Powers", Paul Kennedy (1989) compares different historical episodes to draw general conclusions. He claims, for example, that "there is detectable a causal relationship between the shifts which have occurred over time in the general economic and productive balances and the position occupied by individual Powers in the international system" (Kennedy 1989, xxii). This kind of reasoning shows that historians not only explain particular events, but also historical trends (Little 2010). The recognition that the study of human history is not only concerned with particulars, but also with generalization and type phenomena has spawned a discussion of social mechanisms and their role in historiography.[4]

In the natural sciences it is even more obvious that narrative explanations are not only concerned with particulars. Currie (2014, 1169), for example, argues that there are narrative explanations that explain a particular event as "an instance of a regularity". He calls these narrative explanations "embedded". As an example, he mentions the ubiquitous glaciation of the earth in the late Neoproterozoic that is explained as an extreme case of a general climatological model (Currie 2014, 1169). Similar to comparative approaches in human history, there are scientific approaches that compare particular events or narratives of particular events to generate more general claims about the phenomena in question (Morgan forthc.). Sea captain Henry Piddington, for example, compared narrative accounts of cyclones to infer their law-like behavior (Bhattacharyya forthc.; see Morgan forthc.). Narratives also deal with laws and regularities. Hopkins (forthc.) points out that narrative explanations in geology are "constrained by physical and chemical laws". His discussion shows that geologists refer to several physical laws in their explanations of particular geological events. He seems to suggest that the role of laws in geology is twofold. On the one hand, geologists appeal to general laws to make sense of the events of interest, and on the other hand their explanations need to be in agreement with accepted natural laws to qualify as plausible explanations, even if the laws are not explicitly mentioned. In a similar vein, Gerhard Schurz (2014) argues that macroevolutionary explanations (e.g., the transition from land mammals to aquatic mammals) are considered inadequate if they don't contain references to evolutionary mechanisms (e.g., the mechanism of selection).

Morgan (2017) puts forward another argument for the claim that narrative explanations are not only concerned with particulars. She argues that aspects of narrative explanations might prove exemplary in various ways. They can be "exemplary as a concrete problem solution that can be extended to give an explanation to similar phenomena elsewhere" (Morgan 2017, 94). As an example, she mentions William Foot Whyte's sociological study of a slum area in Boston (Morgan 2017, 87). Morgan (2017, 94) argues that by conceptualizing the slum community as a society (Street

[4] See Plenge (2014) for an overview.

Corner Society), Whyte had "changed the way other social scientists interpreted and understood 'slums'" and that *society* "very rapidly became the new term that 'explained' other such communities". A narrative explanation can also be "exemplary as a method of approach that can be used at other sites" (Morgan 2017, 94). In other words, the methodological approach of a study might be used to construct an explanation of similar phenomena elsewhere.

To sum up, narrative explanations explain how and why things came to be as they are by referencing a series of events that brought about the phenomenon of interest. They can only be known retrospectively and account for contingent outcomes. The difference-making events in a narrative explanations are contingent *per se*, meaning that they were not bound to occur. Narrative explanations are coherent accounts that revolve around a central subject and are constructed by ordering of materials and showing how the pieces fit together. Although narrative explanations explain particulars, there are different ways in which they deal with generalization, regularities and type phenomena.

Reconstructing past evolution: Phylogeography of *Staphylococcus aureus*

Common examples of narrative explanations in evolutionary biology are accounts of the evolution of a trait (e.g., insect wings, flatfish eyes, migrating behavior; see Ereshefsky and Turner 2020; Beatty forthc.; Carrier et al. 2021). In this section I present an account of the evolution and geographic dissemination (phylogeography) of *Staphylococcus aureus* (*S. aureus*) as another example for narrative explanation in evolutionary biology. I show that this explanation is captured well by established accounts of narrative explanation and add another characteristic of narrative explanations that has not received any attention so far, namely that they are instances of (implicit) abstract event structures, i.e., sequences of type events.

In a paper entitled "Origin, evolution, and global transmission of community-acquired *Staphylococcus aureus* ST8" Lena Strauß and collaborators (2017) present the results of a phylogeographic study of *S. aureus*, an opportunistic bacterium. The aim of the study was to reconstruct the molecular evolution and global dissemination of *S. aureus* sequence type[5] (ST) 8. (Strauß et al. 2017). To this end, the researchers used 224 ST8 isolates from different countries collected between the years 1957 and 2013 (Strauß et al. 2017). Strauß and collaborators (2017) were particularly interested in USA300, a hypervirulent and multidrug-resistant clonal *S. aureus* lineage. Their study included the selection of bacterial isolates, whole genome sequencing, phylogenetic analysis, ancestral dating and phylogeographic analysis to answer several interconnected research questions, e.g., 'When and where did ST8 originate?', 'How did ST8 evolve?', and 'How did the global transmission of ST8 occur?'. In addition to the time and place of origin, the answers to these questions include a

[5] Multilocus sequence typing (MLST) is a method of DNA profiling for characterizing isolates of a bacterial species (Maiden et al. 1998). Through MLST different sequence types of *E. coli* can be identified (Doumith et al. 2015). It is thus a way of classifying microbes below the species level.

temporal series of genetic and phenotypic changes as well as the pathway of global transmission of ST8:

> [O]ur results suggest an emergence of ST8 in Europe during the mid-19th century […]. Around 1900 […], the shortened *cap5D* allele […] arose and spread in the European ST8 population. In the early 20th century, one *cap5D*-mutated European ST8 MSSA[6] strain was exported to the United States, where it spread and diversified before eventually evolving into the epidemic USA300 clone by stepwise acquisition of PVL[7], ACME[8], and the *cap5E*[9] mutation […]. Later, this clone was reintroduced to Europe on multiple occasions. Before the spread of the mutated *cap5D*[10] in the European ST8 population, one isolate with WT[11]*cap5D* was exported to Gabon around 1920 and founded a symplesiomorphic, mainly 'African' ST8 sublineage […]. 'Symplesiomorphic' means that this group does not possess any 'derived' characteristics, like PVL or ACME, but represents the state of the common ancestor. The African clone spread and diversified in the Gabonese population and was transmitted to other SSA countries, including Côte d'Ivoire, the Democratic Republic of Congo, and Tanzania, as well as to Australia and Trinidad and Tobago […]. (Strauß et al. 2017, E10600)

In the narrative explanation provided by the scientists, the explanandum is the current state of the ST8 clade and the explanans is a temporal sequence of events. Unlike historical explanations in other fields of biology like developmental biology and evo-devo, this explanation is a population-level explanation that deals with transgenerational processes (see Griesemer 2002; Calcott 2009). The case illustrates how scientists provide a backstory that starts at an earlier point in time and includes a series of events that have brought about the current state of an entity. The oldest ST8 isolate used by Strauß et al. (2017) was collected in 1957, but the narrative of the origin, evolution, and global dissemination of ST8 starts in the mid-nineteenth century when ST8 emerged.[12] It is clear that the narrative could only be known retrospectively. In the mid-nineteenth century, one could not have known how exactly the molecular evolution and global dissemination of ST8 would proceed. The explanation also contains some explicitly narrative sentences like "our results suggest an emergence of ST8 in Europe during the mid-19th century" and "one isolate with WT[13]*cap5D* was

[6] MSSA = methicillin-susceptible *S. aureus*. Methicillin is an antibiotic.

[7] PVL = Panton–Valentine leucocidin, a toxin associated with increased virulence

[8] ACME = arginine catabolic mobile element, a mobile genetic element associated with virulent methicillin-resistant *S. aureus*

[9] *Cap5E* is a gene.

[10] *Cap5D* is a gene.

[11] WT = wild-type (gene), unmutated gene

[12] The researchers used methods of ancestral dating based on mutation rates and phylogenetic analysis to calculate the timing of diversification events and common ancestors (for details see Strauß et al. 2017, E10603).

[13] WT = wild-type (gene), unmutated gene.

exported to Gabon around 1920 and founded a symplesiomorphic, mainly 'African' ST8 sublineage". In their explanation the scientists mention events that are contingent *per se* and made a difference to the outcome, for example, phenotypic and genotypic changes like the acquisition of PVL and the *cap5E* mutation that contribute to the increased virulence of USA300. The sequence of intermediate events makes earlier and later stages in the evolution of ST8 comparable (e.g., with respect to the degree of pathogenicity).

The narrative explanation provided by Strauß et al. (2017) revolves around a central subject, namely the ST8 clade with particular emphasis on the USA300 clonal lineage. This case illustrates the importance of ordering in narrative reasoning. In phylogenetic analysis the sequences are ordered in terms of similarity to create a temporal order. This approach rests on the assumption that populations become increasingly different from each other after divergence, meaning that the more time has passed after divergence, the more differences one can find between the populations; and the more similar the genomes of two populations are, the closer they are related to each other. In phylogenetic analysis, the ordering is done by a software that uses algorithms to reconstruct phylogenies that show how the populations in question are related to each other.[14] The ST8 isolates are spatially connected but also unified by common ancestry and evolutionary processes.

Although the explanation of the molecular evolution and global dissemination of ST8 is a narrative of particular populations and particular events, it deals not only with particulars. For example, it makes implicit and explicit use of common scientific concepts like *pathogen*, *gene*, *mutation*, *lineage* and *clone*. The particulars mentioned in the narrative are instances of these concepts (e.g., USA300 is a clonal lineage; *cap5E* is a gene). Like the narrative explanation of the history of the Ivory Tower as a figure of speech, the global dissemination of ST8 is conceptualized as an instantiation of a broader phenomenon, namely pathogen dissemination and evolution. It is also implied that the event types that are instantiated in the explanation are connected through what I will call *abstract event structures*.[15] Abstract event structures are sequences of type events that typically lead to the occurrence of certain type phenomena. The sequences of particular events that explain the current state of ST8 are instantiations of abstract event structures.

An example for an abstract event structure is the following sequence: A single introduction event (e.g., due to few travel and trade links between countries) followed by local diversification and regional spread typically leads to lower genetic diversity in these regions. In the study by Strauß et al. (2017) this abstract event structure is instantiated by ST8 isolates that were introduced to the Caribbean and Africa. The result of these introduction events followed by local diversification and regional spread of ST8 is relatively low genetic diversity in the respective areas. This series of events explains why ST8 "isolates from the Caribbean and Africa were exclusively found in distinct 'regional' monophyletic[16] branches at distant positions"

[14] See Kranke (forthc.) for a detailed discussion of phylogenetic analysis in the context of narrative science.

[15] I thank Robert Meunier for pointing this aspect out to me.

[16] Monophyletic groups consist of an ancestral population and all of its descendants.

of the phylogeny (Strauß et al. 2017, E10601; see Fig. 1). Instantiations of this type of abstract event structure can also be found in phylogeographic accounts of other clades. Another example of an abstract event structure are the subsequent events of gene acquisitions, altered gene regulation and protein sequence divergence that can lead to increased virulence of bacterial pathogens. These three types of evolutionary events are instantiated in the evolution of the hypervirulent and multidrug-resistant USA300 clonal lineage (Thurlow et al. 2012). Some instances of these type events are mentioned in the explanation provided by Strauß et al. (2017), for example, the acquisition of the mobile genetic element ACME. Thus, although the explanandum phenomena of narrative explanations are conceptualized as particulars that are the result of sequences of particular events, there exists an underlying multiply realizable abstract event structure that often remains implicit in narrative explanations. This point is important to understand how narrative explanations and historical explanations of type phenomena complement each other (see last section) (Fig. 1).

At the end of their paper, the scientists emphasize that their methodological approach can be used to construct narrative explanations of the transmission routes of other pathogens: "This is a good example of how WGS [whole genome sequencing] on global collections may help facilitate epidemiological reconstructions and outbreak surveillance in the future" (Strauß et al. 2017, E10601). Thus, the methodological approach to reconstruct the global dissemination of ST8 might prove exemplary for the construction of narrative explanations of pathogen transmission routes elsewhere. The narrative explanation of the evolution of ST8 by Strauß et al. (2017) is also a particular account of a general version of narrating genetic evolution (Morgan forthc.). This means that phylogenetic or phylogeographic accounts of other clades follow similar rules and conventions.

My analysis shows that the narrative explanation of the evolution and dissemination of ST8 is captured well by established accounts of narrative explanation as it exhibits all the characteristics that I have discussed in the previous section. However, as I have argued in this section the existence of an implicit underlying abstract event structure that is instantiated by sequences of particular events is an additional important characteristic of narrative explanations that has not received sufficient attention so far. It is another aspect of narrative explanations that supports the claim that they not only deal with particulars, but also with type phenomena and generalization. In

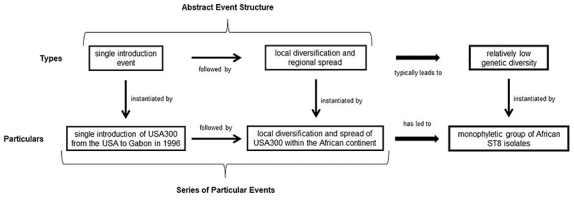

Fig. 1 A series of particular events as an instantiation of an abstract event structure. The boxes at the top represent connected type events that typically lead to a type phenomenon. The boxes at the bottom represent connected particular events in the evolution and dissemination of ST8 that have led to a particular state of the ST8 clade (see Strauß et al. 2017, E10601).

the following section I present and analyze a case of another historical explanation to show that there are historical explanations in evolutionary biology that cannot be captured by existing accounts of time-sequenced narrative explanation, mainly because the explanandum phenomenon is conceptualized as a type phenomenon instead of a particular entity or event.

Studying the processes of evolution: experimental evolution of immunological specificity

In this section I discuss an experimental evolution study by Kevin Ferro and collaborators (2019) that deals with the evolution of immunological specificity. The researchers conducted a laboratory evolution experiment using red flour beetle (*Tribulium castaneum*) populations to answer the questions whether immunological specificity can evolve within a short period and how it arises (Ferro et al. 2019). Insects have an immune system similar to the innate immune system of vertebrates, but do not have an equivalent system to the adaptive immune system of vertebrates which is associated with immune memory and specificity (Sheehan et al. 2020). However, the immune system of some insects shows a form of immune memory called *immune priming*. In the process of immune priming, "prior exposure to a non-lethal inoculum of a pathogen, pathogen-derived material or stress event stimulates the immune response to render the insect resistant to a normally lethal infection a short time later" (Sheehan et al. 2020, 240). Studies have shown that this immune response can be either specific or unspecific (see references in Ferro et al. 2019), meaning that the degree to which the immune system differentiates between different antigens varies.

Experimental evolution is an approach that allows researchers to study evolutionary processes in real-time in a partially controlled setting (Kawecki et al. 2012). In these real-time evolution experiments populations are studied across multiple generations (Rose and Garland 2009, 6). They often involve the creation of a series of evolutionary lines that are exposed to a novel environment (Desjardins et al. 2021). A well-known laboratory evolution experiment is Richard Lenski's *E. coli long-term experimental evolution project* (LTEE) at the University of Michigan. To study bacterial evolution in the laboratory, the researchers created twelve genetically identical populations of *Escherichia coli* (*E. coli*) from a common ancestral clone and let them evolve (Lenski et al. 1991).

For their study of the evolution of immunological specificity Ferro and collaborators (2019) created 24 lines of *Tribolium castaneum* (*T. castaneum*) for different selection and control treatments and let them evolve over 14 generations. They primed the beetle larvae with six different heat-inactivated bacterial species and strains[17] and challenged them with live bacteria. Their selection protocols were designed to either decrease or increase immunological specificity. To select for specificity, they used the same type of bacterium for priming and challenge within generations, but different bacteria species across generations. To select for unspecific immune responses

[17] The researchers used the bacteria *Pseudomonas fluorescens*, *Lactococcus lactis*, and 4 strains of *Bacillus thuringiensis*.

(broad-range immune response), they primed the larvae with one type of bacterium, but challenged them with a different type of bacterium within and across generations (Ferro et al. 2019, 20,599). After 14 generations of laboratory evolution, the researchers performed phenotypic analysis (assessment of survival, development, fecundity) and conducted transcriptomic analysis to assess the genetic basis (gene expression) of immune priming and specificity (Ferro er al. 2019, 20,599). The results of the study are presented as follows:

> Our study reveals that selection for immunological specificity over a rather small number of 14 generations already results in strongly differing transcriptional responses upon immune priming. These differences correspond to survival benefits during a subsequent infection. This demonstrates a general evolutionary responsiveness of a phenotypically plastic system that provides immune memory. Moreover, the evolutionary changes appear to be targeted at a limited set of pathogens; we observed that selection aiming at a generally higher degree of specificity yielded a more pronounced primed immune response for one bacterial species, the entomopathogen[18] *B. thuringiensis*. […] Evolution of increased priming responses were restricted to *B. thuringiensis* but did not extend to the other tested bacterial species. This suggests that priming specificity and its evolvability might be related to the likelihood of infection or coevolution with a certain pathogen. […] The transcriptomic signature of priming in the evolved beetles supported the observed enhanced specificity toward *B. thuringiensis* and suggests that immune priming consists of divergent sets of genes that confer general priming and bacteria-specific responses, respectively. […] The divergent transcriptome signatures for the specific vs. unspecific selection treatments […] suggest that the microevolution of specificity relies on changes in metabolism, which is often a deciding factor in the outcome of host-pathogen interactions […], and immunity. (Ferro et al. 2019, 20601-2)

The scientists explain immunological specificity by showing how the phenomenon is brought about but also show how it does not arise. The study suggests that a higher degree of specificity only evolves in coevolution with one bacterial species (*B. thuringiensis*) but does not arise in coevolution with other bacteria. The scientists' main interest is not the genetic mechanism of immunological specificity but the question whether, how and how fast the mechanisms that realize immunological specificity arise. Thus, they are primarily concerned with the history of the genetic mechanisms that realize immunological specificity. However, the experiment also provides insights into coevolutionary dynamics (Peuß, personal communication, 24.02.2021). Although many experimental evolution studies are set out to study how a certain type of biological function arises[19], there are other such experiments that are

[18] Entomopathogen = insect pathogen

[19] See for example, Maeda et al. 2020 (antibiotic resistance), Wei et al. 2014 (enhanced pathogenicity), Gervasi and Schiestl 2017 (plant adaptation to pollinators).

not designed to bring about a certain function or phenomenon. The initial goal of the LTEE, for example, was to study long-term evolutionary dynamics.

Laboratory evolution experiments are understood as model systems. The experimental evolution study conducted by Ferro et al. (2019) is a model in two respects. First, *T. castaneum* is a model organism used in different fields like evolutionary biology, genetics, developmental biology, and environmental studies (Adamski et al. 2019; Wang et al. 2007; Fedina and Lewis 2008). Scientists study model organisms in the hope that knowledge (e.g., data, theories, methods) gained by studying the model can be extrapolated to other organisms (Ankeny and Leonelli 2021, 2). In this case an extrapolation of knowledge to and from studies of other organisms might be possible because the gene regulatory mechanisms that bring about immunological specificity are similar in red flour beetles, mice, and humans (Peuß, personal communication 24.02.2021). Second, and more importantly, the experiment itself is a model. Emily Parke (2014), for example, argues that laboratory evolution experiments are models with a dynamic temporal element (see also Weber 2014, 759). Marcel Weber (2014, 757) uses the term 'experimental modelling' to refer to model systems that use living organisms to recreate or simulate biological processes. Biologist Thomas Flatt (personal communication 13.07.2018) agrees with the characterization of laboratory evolution experiments as models and argues that they are simplified systems: "[Y]ou can control things, you can maybe isolate certain causal factors […], but of course you also know in the back of your head, that you're sacrificing a little bit of, let's say, ecological or biological realism by doing this, because you're filtering out a lot of other influences". Like other models, laboratory evolution experiments are idealized systems that reduce the complexity of evolutionary processes in nature to be able to study specific aspects of evolutionary dynamics (Weber 2014, 765). Ferro and collaborators (2019) designed their experiment to study a particular type of evolutionary transition, namely the occurrence of immunological specificity. In their experiment the evolutionary processes that occur in the experimental *T. castaneum* populations "stand in" for other physically distinct kinds of processes in other systems (see Weber 2014). Immunological specificity cannot only evolve in *T. castaneum* but also in other species in the laboratory and in nature in coevolution with different pathogens. The particular organisms that are used in the experiment thus represent types, e.g., *T. castaneum* populations represent host populations and the different bacterial species and strains represent different types of pathogens.

Parke (2014) presents a similar argument for the LTEE. However, she argues that depending on the kinds of inferences drawn from the study, the experimental *E. coli* populations stand in for different types (Parke 2014, 524). In three of the 12 *E. coli* populations, the researchers observed an increase in mutation rates (Sniegowski et al. 1997). From their observation in the laboratory, they make an inference about natural populations of pathogenic *E. coli* and *Salmonella* and argue that high mutation rates in these natural populations might evolve through the same evolutionary mechanism that they found in the laboratory populations (Parke 2014, 522). In this case the laboratory populations represent a certain type of pathogenic bacterium. Another observation that the scientists made in the experimental *E. coli* populations is a step-like increase in cell size (Elena et al. 1996). They interpret this process as an instance of

"punctuated evolution", also called *punctuated equilibrium*.[20] The scientists argue that the punctuated changes in the experimental *E. coli* populations are associated with rare events of fixation of beneficial mutations and argue that cases of punctuated evolution in the fossil record could also be explained by this process (Elena et al. 1996, 1804). In this case the laboratory *E. coli* populations stand in for populations with a certain type of evolutionary history (isolated episodes of change after periods of stasis). This could be any species from any branch of the phylogenetic tree that shares certain properties of its evolutionary history with the laboratory *E. coli* populations (Parke 2014, 524; see following section for the discussion of an example).

Narrative explanations and historical explanations of type phenomena

In this section I compare the explanation of the evolution of immunological specificity with the explanation of the evolution and dissemination of ST8 to show the similarities and differences between narrative explanations and historical explanations of type phenomena in evolutionary biology. I will argue that the two kinds of explanation are similar in many ways but differ with respect to their focus on either particulars or type phenomena.

Like the explanation of the evolution and dissemination of ST8, the explanation of the evolution of immunological specificity deals with transgenerational processes and is a population-level explanation. It also references a temporal series of events that brought about the explanandum phenomenon. The cases that I have discussed in the previous sections show that historical explanations of type phenomena cover shorter time spans than narrative explanations. The reason for this difference is that constructing explanations of type phenomena involves studying known temporal sequences of events whereas the temporal sequences of events in narrative explanations are reconstructed from traces. Individual scientists or research teams can observe evolutionary trajectories in the laboratory or in the field for decades but sequences of evolutionary relevant events of the distant past (e.g., millions of years ago) cannot be observed but are reconstructed from clues.[21] The data that Ferro et al. (2019) used for their analysis encompass a period of over three years while the narrative explanation provided by Strauß et al. (2017) covers a time span of 159 years. However, other narrative explanations in evolutionary biology can encompass a period of several million years of evolution. The LTEE as the longest laboratory evolution experiment so far is running for over 33 years. However, knowledge of

[20] 'Punctuated equilibrium' is concept of speciation chiefly defended by Niles Eldregde and Stephen Jay Gould (1972). Eldredge and Gould (1972, 115) contrast their concept with "phyletic gradualism", the idea that speciation occurs through gradual change of populations and argue that instead "speciation is a rare and difficult event that punctuates a system in homeostatic equilibrium".

[21] Reconstruction of events can also play a role in experimental evolution studies, for example in the form of "going back" to earlier states by reexamining frozen samples of earlier laboratory populations. However, in these cases, the temporal order is still known, not inferred from clues.

evolutionary pathways is not only produced in the laboratory but can also result from field experiments[22] or long-term observations of natural processes[23].

In most cases, historical explanations of type phenomena are also more fine-grained than narrative explanations as the intervals between the events of a sequence are relatively short. Studying real-time evolution usually involves tracking of phenotypic and genetic changes in short intervals. Ferro et al. (2019) tested for immune priming after 7 and 14 host generations but there are also laboratory evolution experiments that track the gradual adaptation of pathogens to changes in the host. In these cases, researchers examine genetic and phenotypic changes in even shorter intervals (see Huang et al. 2017 for an example). Elena et al. (1996, 1802) measured the mean fitness of the laboratory *E. coli* populations every 100 generations, a rather short interval compared to sequences of narrative explanations of microbial evolution. For instance, the events in the narrative explanation of the evolution and dissemination of ST8 are several years, sometimes decades, apart which corresponds to ten thousands or even hundred thousands of generations. In narrative explanations of vertebrate evolution, the events of a temporal series are usually millions of years apart which corresponds to ten thousands of generations for organisms with relatively long generation times. The temporal series of narrative explanations in evolutionary biology usually only contains a few important events in relatively large intervals. Of course, the number of events that are included in narrative explanations depends on the research question, but usually the researchers only reconstruct a relatively small number of significant events.

In experimental evolution studies, the outcome is contingent upon the series of events that connects the outcome with the starting point (Desjardins 2011, 360). The comparison of different selection and control treatments in the study by Ferro et al. (2019) shows that the evolution of immunological specificity is contingent upon prior events (e.g., exposure to a certain pathogen). Similarly, the occurrence of increased mutation rates and punctuated evolution in the LTEE is contingent upon prior events. Thus, just like narrative explanations, historical explanations of type phenomena account for contingent phenomena in this sense. However, while the difference-making events in narrative explanations are contingent *per se* (not bound to occur), they are not necessarily contingent in historical explanations of type phenomena. Whether the difference-making events are contingent *per se* depends on the research question and experimental design. Ferro and collaborators (2019) for example, have brought about the events that have eventually led to the evolution of immunological specificity (priming and challenge with the same bacteria species within generations). The experiment was designed to bring about this phenomenon. In the LTEE, however, the events that have led to punctuated evolution (beneficial mutations and their fixation) were not bound to occur exactly as they have occurred. Because of these differences between experimental evolution studies, contingency of difference-making events cannot be used as a criterion to distinguish between narrative explanations and historical explanations of type phenomena.

[22] For a general discussion of experimental evolution in the field see Irschick and Reznick (2009). For examples see Zbinden et al. (2008) and Reznick et al. (1990).

[23] See Leray et al. (2021) for a discussion of this long-term monitoring of marine ecosystems.

The research activities that generate the respective explanations considerably differ from one another. While time-sequenced narrative explanations in evolutionary biology result from reconstructing past evolution, the explanation of the evolution of immunological specificity was generated by constructing sequences of events to bring about a phenomenon. The former involves temporal ordering of materials and showing how they fit together. In laboratory evolution experiments, however, the temporal order of important events is known and to a certain extent manipulated by the researchers. Thus, the researchers' central task is not to reconstruct an evolutionary pathway through ordering, but to study whether and/or how and why a certain phenomenon has occurred at the end of an evolutionary pathway. Depending on the experimental design, the researchers induce the important events themselves (e.g., priming of beetles through expose to a pathogen) and/or they monitor the changes regularly (e.g., sequence analysis of viruses after each passage). Particularly in cases where the changes are monitored in larger intervals, the researchers might not know the exact time where a change has occurred, but the temporal order of crucial events is known. Thus, historical explanations of type phenomena are constructed by studying known histories (sequences of events).

The temporal sequences of the two kinds of historical explanation both include particulars such as organisms and events (e.g., ST8 populations, *cap5E* mutation; laboratory *T. castaneum* populations, exposure to laboratory *B. Thuringiensis* populations). In both cases these temporal sequences of particulars instantiate or represent abstract event structures that bring about a multiply realizable phenomenon (e.g., relatively low genetic diversity; immunological specificity). While the underlying abstract event structure often remains implicit in narrative explanations, it is more obvious in historical explanations of type phenomena that the sequences of particular events represent types. For example, in the explanation of immunological specificity the particular entities (e.g., laboratory *T. castaneum* and bacteria populations) and particular events (challenge of laboratory *T. castaneum* populations with laboratory *B. thuringiensis* populations) of the experiment are understood as representations of types of entities (host, pathogen) and events (priming and challenge of a host with a certain type of pathogen). I have argued that both philosophers of science and scientists think of experimental evolution studies as models that represent multiply realizable phenomena. This difference already becomes obvious when we compare the titles of the two papers that I have discussed in the previous sections. The paper by Strauß and collaborators (2017) is entitled "Origin, evolution, and global transmission of community-acquired *Staphylococcus aureus* ST8" while the title of Ferro et al.'s (2019) paper is "Experimental evolution of immunological specificity". The temporal and spatial evolutionary pathway described by Strauß et al. (2017) is unique to the ST8 clade and occurred only once. The evolution of immunological specificity, on the other hand, is a phenomenon that can occur in different species at different times and places. Ferro et al. (2019) are clearly concerned with the evolution of immunological specificity in a more general sense, not merely with its occurrence in the laboratory populations of *T. castaneum*.

Muhammad Khalidi (2021) has recently proposed a distinction between token-etiological kinds and type-etiological kinds that helps understand how the explananda of narrative explanations and historical explanations of type phenomena are concep-

tualized. According to Khalidi (2021, emphasis omitted) "(t)oken-etiological kinds have members who all originate in the very same event or have followed the same token causal trajectory or share the selfsame history". The ST8 clade in the narrative explanation provided by Strauß et al. (2017) is an example of a classification of the explanandum phenomenon as token-etiological kind. As I have argued, the scientists are mainly interested in the particular history of the ST8 clade and all members of the clade (different ST8 lineages) share the same token origin (common ancestor). Khalidi (2021) notes that token-etiological kinds like species or languages with a common origin can also be conceived of as individuals rather than kinds. In fact, in some discussions of narrative explanations, particularly those who refer to the concept of *central subject*, the authors understand these entities as individuals rather than kinds. Immunological specificity, on the other hand, is a type-etiological kind. Type-etiological kinds "do not share the very same token origin or history but rather the same type of origin or history. Their members do not originate in the same event or follow the very same causal pathway; rather their origins or histories are tokens of the same type." (Khalidi 2021). I have argued that the researchers understand immunological specificity as a multiply realizable phenomenon with a certain type of history. The particular histories of the laboratory flour beetle populations that exhibit immunological specificity are understood as tokens of this type. Similarly, the occurrences of immunological specificity in the laboratory flour beetle populations are seen as tokens of a type of phenomenon.[24] As I have argued in the previous section, the explanation of the evolution and dissemination of ST8 explains the current state of a particular entity, but also deals with type phenomena. The explanation of the evolution of immunological specificity, on the other hand, explains a type phenomenon, but is also concerned with particulars that are understood as instances of a type. In a way, historical explanations of type phenomena deal with central subjects (individuals; e.g., laboratory *E. coli* or *T. castaneum* lines), but the explanandum itself is conceptualized as a multiply realizable phenomenon.

The central difference between narrative explanations and historical explanations of type phenomena lies in the conceptualization of the explanandum phenomenon as a token-etiological kind or type-etiological kind, respectively. Both kinds of explanation deal with particulars and type phenomena but differ with respect to their focus. In this sense, the two kinds of historical explanation are like two sides of the same coin. Narrative explanations focus on the particularity or uniqueness of entities and events while historical explanations of type phenomena focus on their typeness or generalizability. However, as I have already argued, the two kinds of explanation are not just two different versions of the same story where one focuses on particulars and the other one on types. Instead, the research questions and activities that produce narrative and historical explanations of type phenomena are different. A narrative explanation is generated by asking how and why something came to be as it is. This question is interesting because the historical pathway is unknown or only partially

[24] It is possible that trained immune response in different species (e.g., animals, plants, bacteria) share a common token origin (Ferro et al. 2019, 20,603). However, whether trained immunity in different species is a result of convergent evolution or has a common origin is not immediately relevant for the research question that Ferro et al. (2019) pursue.

known. The researchers' central task is thus to reconstruct the pathway from clues. The result is an explanation that provides a temporal series of events. A historical explanation of a type phenomenon, however, is generated by asking how and why a type of phenomenon arises. To answer this question, the researchers study known historical pathways and identify typical patterns of events or causal factors that bring about the phenomenon of interest.

I have argued that the two kinds of historical explanation explain different aspects of evolution. While narrative explanations explain how and why a particular trait or species came to be as it is, historical explanations of type phenomena explain multiply realizable evolutionary dynamics and transitions. Thus, they are not competing explanations of the same explanandum phenomenon but complement each other. The following example illustrates this point. Ana Millanes and collaborators (2011) have reconstructed the phylogeny of jelly fungi to reexamine their classification and to examine character evolution within this group. In their narrative explanation of the evolution of different morphological characters, they refer to the concept of punctuated evolution and cite the paper by Lenski and collaborators (Millanes et al. 2011, 25–26). Millanes et al. (2011, 26) argue that change in one particular morphological character (basidium habit)[25] of jelly fungi "is consistent with a punctuated mode of evolution", meaning that the character has not changed gradually but during isolated episodes after a period of stasis. Based on the results of the LTEE the researchers hypothesize that "this trait might have been subject to positive selection, at least periodically" (Millanes et al. 2011, 26). In this case the explanation of how punctuated evolution occurs has helped Millanes and collaborators to make sense of the results of their phylogenetic analysis and generate a hypothesis of the evolution of basidium morphology in jelly fungi. The example shows that the two kinds of explanation can easily be integrated and support each other. On the one hand, the LTEE provides an abstract event structure that helps explain the morphological evolution of jelly fungi. On the other hand, the interpretation of the evolution of basidium morphology in jelly fungi as another instance of punctuated evolution suggests that this phenomenon not only exists in laboratory *E. coli* populations but also in fungi and is thus generalizable. More generally, in cases where parts of the underlying abstract event structure of narrative explanations are made explicit, historical explanations of type phenomena can provide the abstract event structure that is instantiated by the particular events of narrative explanations.

Acknowledgements I would like to thank Thomas Flatt and Rob Peuß for their time and patience. Talking to them about their work was extremely helpful and fun. I have presented an earlier version of this work at the *EvoPAD* colloquium at the University of Münster and thank the participants for their questions and careful comments. Thanks to Ulrich Krohs, Robert Meunier and Fridolin Gross for their advice and feedback. I also thank Emily Parke and two anonymous referees for their helpful comments and suggestions. Last but not least, I am grateful to Oliver Höltker for his assistance.

Funding: My research leading to these results was funded by the German Research Foundation (DFG) - 281125614 / GRK2220.

Open Access funding enabled and organized by Projekt DEAL.

[25] A basidium is a spore-bearing structure.

Availability of data and material: Not applicable.

Code Availability Not applicable.

Declarations

Conflicts of interest/competing interests: No conflicts of interest/competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Adamski Z, Bufo SA, Chowański S et al (2019) Beetles as Model Organisms in Physiological, Biomedical and Environmental Studies – A Review. Front Physiol 10. https://doi.org/10.3389/fphys.2019.00319

Ankeny RA, Leonelli S (2021) Model Organisms. Cambridge University Press, Cambridge

Beatty J (2017) Narrative possibility and narrative explanation. Studies in History and Philosophy of. Sci Part A 62:31–41. https://doi.org/10.1016/j.shpsa.2017.03.001

Beatty J (forthc.) Narrative Solutions to a Common Evolutionary Problem. In: Morgan MS, Berry DJ, Hajek KM (eds) Narrative Science: reasoning, representing and knowing since 1800. Cambridge University Press, Cambridge

Beatty J (2016) What are narratives good for? Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological. Biomedical Sci 58:33–40. https://doi.org/10.1016/j.shpsc.2015.12.016

Bhattacharyya D (forthc.) From Memories to Forecasting: Narrating Imperial Storm Science. In: Morgan MS, Berry DJ, Hajek KM (eds) Narrative Science: reasoning, representing and knowing since 1800. Cambridge University Press, Cambridge

Calcott B (2009) Lineage Explanations: Explaining How Biological Mechanisms Change. Br J Philos Sci 60:51–78

Carrier M, Mertens R, Reinhardt C (2021) Introduction. In: Carrier M, Mertens R, Reinhardt C (eds) Narratives and Comparisons: Adverseries or Allies in Understanding Science. Bielefeld University Press, transcript, Bielefeld, pp 7–28

Cleland CE (2002) Methodological and Epistemic Differences between Historical Science and Experimental Science. Philos Sci 69:447–451. https://doi.org/10.1086/342455

Currie AM (2014) Narratives, mechanisms and progress in historical science. Synthese 191:1163–1183. https://doi.org/10.1007/s11229-013-0317-x

Currie AM (2018) Rock, Bone and Ruin: An Optimist's Guide to the Historical Sciences. MIT Press, Cambridge

Danto AC (1968) Analytical Philosophy of History, paperback edition. Cambridge University Press, London, New York

Danto AC (1985) Narration and Knowledge. Columbia University Press, New York

Danto AC (1962) Narrative Sentences. History and Theory 2:146–179. https://doi.org/10.2307/2504460

Desjardins E (2011) Historicity and experimental evolution. Biol Philos 26:339–364. https://doi.org/10.1007/s10539-011-9256-4

Desjardins E, Kurtz J, Kranke N et al (2021) Beyond Standardization: Improving External Validity and Reproducibility in Experimental Evolution. Bioscience 71:543–552. https://doi.org/10.1093/biosci/biab008

Doumith M, Day M, Ciesielczuk H et al (2015) Rapid Identification of Major Escherichia coli Sequence Types Causing Urinary Tract and Bloodstream Infections. J Clin Microbiol 53:160–166. https://doi.org/10.1128/JCM.02562-14

Eldredge N, Gould SJ (1972) Punctuated Equilibria: An Alternative to Phyletic Gradualism. In: Schopf TJM (ed) Models in Paleobiology. Freeman, Cooper and Company, San Francisco, pp 82–115

Elena SF, Cooper VS, Lenski RE (1996) Punctuated Evolution Caused by Selection of Rare Beneficial Mutations. Science

Ereshefsky M, Turner D (2020) Historicity and explanation. Studies in History and Philosophy of. Sci Part A 80:47–55. https://doi.org/10.1016/j.shpsa.2019.02.002

Fedina TY, Lewis SM (2008) An integrative view of sexual selection in Tribolium flour beetles. Biol Rev 83:151–171. https://doi.org/10.1111/j.1469-185X.2008.00037.x

Ferro K, Peuß R, Yang W et al (2019) Experimental evolution of immunological specificity. PNAS 116:20598–20604. https://doi.org/10.1073/pnas.1904828116

Gervasi DDL, Schiestl FP (2017) Real-time divergent evolution in plants driven by pollinators. Nat Commun 8:14691. https://doi.org/10.1038/ncomms14691

Ginzburg C (1979) Clues: Roots of a Scientific Paradigm. Theory and Society 7:273–288

Glennan S (2010) Ephemeral Mechanisms and Historical Explanation. Erkenn 72:251–266. https://doi.org/10.1007/s10670-009-9203-9

Griesemer JR (1996) Some concepts of historical science. Memorie della Societa Italiana de Scienze Naturali e del Museo Civico di Storia Naturale di Milano 28:60–69

Griesemer JR (2002) Space Time: Temporality and Attention in Iconographies of the Living. In: Schmidgen H (ed) Experimental Arcades: The Materiality of Time Relations in Life Sciences, Art, and Technology (1830–1930). Max Plank Institut f?r Wissenschaftsgeschichte, Berlin, p Preprint 226: 45–57

Haines E (forthc.) Visual Evidence and Narrative in Botany and War: Two Domains, One Practice. In: Morgan MS, Berry DJ, Hajek KM (eds) Narrative Science: reasoning, representing and knowing since 1800. Cambridge University Press, Cambridge

Hajek KM (forthc.) Mass Extinctions and Narratives of Recurrence. In: Morgan MS, Berry DJ, Hajek KM (eds) What is Narrative in Narrative Science? The Narrative Science Approach. Cambridge University Press, Cambridge

Harrison P, Hesketh I (2016) Introduction: Evolution and historical explanation. Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological. Biomedical Sci 58:1–7. https://doi.org/10.1016/j.shpsc.2015.12.010

Hopkins AE (forthc.) The Narrative Nature of Geology and the Rewriting of the Stac Fada Story. In: Morgan MS, Berry DJ, Hajek KM (eds) Narrative Science: reasoning, representing and knowing since 1800.Cambridge University Press, Cambridge

Huang DT-N, Lu C-Y, Chi Y-H et al (2017) Adaptation of influenza A (H7N9) virus in primary human airway epithelial cells. Sci Rep 7:11300. https://doi.org/10.1038/s41598-017-10749-5

Hull DL (1975) Central Subjects and Historical Narratives. History and Theory 14:253–274. https://doi.org/10.2307/2504863

Huss J, Morgan MS, Berry DJ, Hajek KM (eds) Narrative Science: reasoning, representing and knowing since 1800.Cambridge University Press, Cambridge

Irschick DJ, Reznick D (2009) Field Experiments, Introductions, and Experimental Evolution: A Review and Practical Guide. In: Garland T, Rose MR (eds) Experimental Evolution: Concepts, Methods, and Applications of Selection Experiments. University of California Press, Berkely, Los Angeles, London, pp 173–194

Kaiser MI, Plenge D (2014) Introduction – Points of Contact between Biology and History. In: Kaiser MI, Scholz O, Plenge D, Hüttemann A (eds) Explanation in the Special Sciences – The Case of Biology and History. Springer, Dordrecht, pp 1–23

Kawecki TJ, Lenski RE, Ebert D et al (2012) Experimental evolution. Trends Ecol Evol 27:547–560. https://doi.org/10.1016/j.tree.2012.06.001

Kennedy P (1989) The Rise and Fall of the Great Powers: Economic Change and Military Conflict from 1500 to 2000. Vintage Books, New York

Khalidi MA (2021) Etiological Kinds. Philos Sci 88:1–21. https://doi.org/10.1086/710020

Kranke N, Morgan MS, Berry DJ, Hajek KM (eds) Narrative Science: reasoning, representing and knowing since 1800.Cambridge University Press, Cambridge

Lenski RE, Rose MR, Simpson SC, Tadler SC (1991) Long-Term Experimental Evolution in Escherichia coli. I. Adaptation and Divergence During 2,000 Generations. Am Nat 138:1315–1341

Leray M, Wilkins LGE, Apprill A et al (2021) Natural experiments and long-term monitoring are critical to understand and predict marine host–microbe ecology and evolution. PLoS Biol 19:e3001322. https://doi.org/10.1371/journal.pbio.3001322
Little D (2010) New Contributions to the Philosophy of History. Springer, Dordrecht
Maeda T, Iwasawa J, Kotani H et al (2020) High-throughput laboratory evolution reveals evolutionary constraints in Escherichia coli. Nat Commun 11:5970. https://doi.org/10.1038/s41467-020-19713-w
Maiden MCJ, Bygraves JA, Feil E et al (1998) Multilocus sequence typing: A portable approach to the identification of clones within populations of pathogenic microorganisms. PNAS 95:3140–3145
Martin W (1968) Recent Theories of Narrative. Cornell University Press, Ithaca, London
Millanes AM, Diederich P, Ekman S, Wedin M (2011) Phylogeny and character evolution in the jelly fungi (Tremellomycetes, Basidiomycota, Fungi). Mol Phylogenet Evol 61:12–28. https://doi.org/10.1016/j.ympev.2011.05.014
Morgan MS (2017) Narrative ordering and explanation. Studies in History and Philosophy of. Sci Part A 62:86–97. https://doi.org/10.1016/j.shpsa.2017.03.006
Morgan MS (forthc.) Narrative: A General Purpose Technology for Science. In: Morgan MS, Berry DJ, Hajek KM (eds) Narrative Science: reasoning, representing and knowing since 1800. Cambridge University Press, Cambridge
O'Hara RJ (1988) Homage to Clio, or, Toward an Historical Philosophy for Evolutionary Biology. Syst Zool 37:142–155. https://doi.org/10.2307/2992272
Parke EC (2014) Experiments, Simulations, and Epistemic Privilege. Philos Sci 81:516–536. https://doi.org/10.1086/677956
Paskins M, Morgan MS, Berry DJ, Hajek KM (eds) Narrative Science: reasoning, representing and knowing since 1800.Cambridge University Press, Cambridge
Patrick L, Gardiner (1961) The Nature of Historical Explanation. Oxford University Press, Oxford
Plenge D (2014) Do Historians Study the Mechanisms of History? A Sketch. In: Kaiser MI, Scholz O, Plenge D, Hüttemann A (eds) Explanation in the Special Sciences – The Case of Biology and History. Springer, Dordrecht, pp 211–243
Reznick DA, Bryga H, Endler JA (1990) Experimentally induced life-history evolution in a natural population. Nature 346:357–359. https://doi.org/10.1038/346357a0
Rose MR, Garland T (2009) Darwin's Other Mistake. In: Garland T, Rose MR (eds) Experimental Evolution: Concepts, Methods, and Applications of Selection Experiments. University of California Press, Berkely, Los Angeles, London, pp 3–14
Roth PA (2017) Essentially narrative explanations. Studies in History and Philosophy of. Sci Part A 62:42–50. https://doi.org/10.1016/j.shpsa.2017.03.008
Schurz G (2014) Evolutionary Explanations and the Role of Mechanisms. In: Kaiser MI, Scholz O, Plenge D, Hüttemann A (eds) Explanation in the Special Sciences – The Case of Biology and History. Springer, Dordrecht, pp 155–170
Shapin S (2012) The Ivory Tower: the history of a figure of speech and its cultural uses. Br J History Sci 45:1–27. https://doi.org/10.1017/S0007087412000118
Sheehan G, Farrell G, Kavanagh K (2020) Immune priming: the secret weapon of the insect world. Virulence 11:238–246. https://doi.org/10.1080/21505594.2020.1731137
Sniegowski PD, Gerrish PJ, Lenski RE (1997) Evolution of high mutation rates in experimental populations of E. coli. Nature 387:703–705. https://doi.org/10.1038/42701
Strauß L, Stegger M, Akpaka PE et al (2017) Origin, evolution, and global transmission of community-acquired Staphylococcus aureus ST8. PNAS 114:E10596–E10604. https://doi.org/10.1073/pnas.1702472114
Thurlow LR, Joshi GS, Richardson AR (2012) Virulence Strategies of the Dominant USA300 Lineage of Community Associated Methicillin Resistant Staphylococcus aureus (CA-MRSA). FEMS Immunol Med Microbiol 65:5–22. https://doi.org/10.1111/j.1574-695X.2012.00937.x
Tucker A (2014) Biology and Natural History: What Makes the Difference? In: Kaiser M, Scholz OR, Plenge D, Hüttemann A (eds) Explanation in the Special Sciences: The Case of Biology and History. Springer, Dordrecht, pp 347–366
Wang L, Wang S, Li Y et al (2007) BeetleBase: the model organism database for Tribolium castaneum. Nucleic Acids Res 35:D476–D479. https://doi.org/10.1093/nar/gkl776
Weber M (2014) Experimental Modeling in Biology: In Vivo Representation and Stand-Ins as Modeling Strategies. Philos Sci 81:756–769. https://doi.org/10.1086/678257
Wei K, Sun H, Sun Z et al (2014) Influenza A Virus Acquires Enhanced Pathogenicity and Transmissibility after Serial Passages in Swine. J Virol 88:11981–11994. https://doi.org/10.1128/JVI.01679-14

White M (1963) The Logic of Historical Narration. In: Hook S (ed) Philosophy and History: A Symposium. New York University Press, New York, pp 3–31

Zbinden M, Haag CR, Ebert D (2008) Experimental evolution of field populations of Daphnia magna in response to parasite treatment. J Evol Biol 21:1068–1078. https://doi.org/10.1111/j.1420-9101.2008.01541.x

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.