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On evolutionary causes and evolutionary processes

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ABSTRACT

In this essay I consider how biologists understand 'causation' and 'evolutionary process', drawing attention to some idiosyncrasies in the use of these terms. I suggest that research within the evolutionary sciences has been channeled in certain directions and not others by scientific conventions, many of which have now become counterproductive. These include the views (i) that evolutionary processes are restricted to those phenomena that directly change gene frequencies, (ii) that understanding the causes of both ecological change and ontogeny is beyond the remit of evolutionary biology, and (iii) that biological causation can be understood by a dichotomous proximate–ultimate distinction, with developmental processes perceived as solely relevant to proximate causation. I argue that the notion of evolutionary process needs to be broadened to accommodate phenomena such as developmental bias and niche construction that bias the course of evolution, but do not directly change gene frequencies, and that causation in biological systems is fundamentally reciprocal in nature.

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A volcano erupts, generating extreme environmental conditions. Magma and hot gasses pour out of the mountainside, and every living creature that the lava stream crosses is demolished. Such eruptions are amongst the most destructive natural disasters known to science. Yet even here we see the evidence of evolutionary adaptation. For instance, an underwater volcano in Guam has been erupting since 2004, and investigations of the marine life near it have revealed unusual varieties of fish, shrimp, crabs and limpets, including several newly identified species (Green, 2009). These organisms thrive in hot water with strong chemicals, for instance, they possess anatomical adaptations that allow them to survive in extremely high sulphide concentrations (Moyes and Schulte, 2007). Seemingly, a history of volcanic eruption in the vicinity has *caused* evolutionary change by leading to the natural selection of organisms able to tolerate or exploit the severe ecological states created.

In common parlance we would feel entirely comfortable speaking of the volcano causing evolution, yet neither volcanoes, nor any other environmental change, are formally recognized as causes of evolutionary change in evolutionary biology textbooks. This is not to suggest that evolutionary biologists fail to appreciate the causal link between environmental change and organismal change: of course they do. That relationship has been well-established since Darwin (1859). Yet the evolutionist would typically make a distinction between those processes that bring about changes in environmental conditions (amongst which they would include volcanic eruptions) and those processes that bring about lasting and heritable changes in organisms through modifying gene frequencies (where volcanoes do not show). For the evolutionary biologist, the *real cause* of those organismal adaptations for tolerance to extreme temperatures and chemical environments is natural selection. Other direct causes of evolution are also recognized, and include random genetic drift, gene flow and mutation. But volcanic eruptions, like all other phenomena that modify the circumstances in which organisms live, are not viewed as evolutionary causes: rather they are background conditions.

This distinction between *a phenomenon that causes an evolutionary process to occur* and *a direct evolutionary cause or process itself*, is a subtle but important one. Volcanic eruptions do not cause organismal change directly (if selections were impeded, for instance, though the absence of heritable variation, no organismal change would arise): rather, they create the conditions under which natural selection may (or may not) ensue.

Note, this is a different description of causality from that found in common parlance, or even in other domains of science. If a nail is hit with a hammer we describe the hammer as the direct cause of the nail entering the wood. It would seem strange to describe the impact of the hammer as a background condition to the nail's momentum. To my knowledge, physicists see no need to distinguish, as categorically different, hammer-moving processes

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from wood-entering processes. Likewise, we would not be optimistic about the chances of the defendant in the dock receiving a 'not guilty' verdict if their defense was based on the argument that they did not cause the death of the victim that they shot – that was the bullet – they only pulled the trigger. In common parlance, the layperson might well describe the volcano as the cause of the Loihi shrimp's unusual physiology, but the professional evolutionist, whilst recognizing the causal connection, would typically not. Perhaps philosophers would point to other differences between these examples, but it is my contention that they are not to be distinguished on logical grounds, but rather by scientific convention.

The convention within evolutionary biology is to distinguish evolutionary processes from the causes or modulators of those processes. A volcanic eruption, like all environmental change, can trigger an evolutionary event to occur, or transform the course of pre-existing evolutionary events, but this does not make it an evolutionary process in itself. Any suggestion that environmental events are evolutionary processes would, it is generally argued, conflate causes of changes in background conditions with the evolutionary processes by which organic changes occur (Scott-Phillips et al., 2014). Eruptions are ecological, not evolutionary, events. They might initiate or change a response to selection, by modifying the relative fitnesses of alternative genotypes, but (even granting that they are indirectly causal) it would be a logical error to view volcanoes as direct causes of evolutionary change. Likewise, population size might modulate the action of genetic drift, but this does not make it an evolutionary process: rather, it is a modulator, or background condition.

I see considerable merit in the aforementioned distinction, but nonetheless suspect that it is more problematical than it first appears. Recently, I have argued that discipline-based scientific fields frequently emerge that by default do not treat potentially relevant phenomena as causes, leading to the neglect of relevant processes (Laland et al., 2011, 2013a,b). A good example is provided by Ernst Mayr's, and the other architects of the Modern Synthesis', 'black boxing' of development (Hamburger, 1980; Amundson, 2005; Laland et al., 2011). Such 'black boxing' or 'screening off' of a phenomenon, and exiling its study to an adjacent discipline, is often initially useful, and may be necessary to make scientific progress. It is only a problem if and when it becomes dogma. I suspect that this has happened with Mayr's (1961) distinction between proximate and ultimate causation: an initially useful heuristic (i.e. that proximate and ultimate explanations are not competing alternatives) has degenerated into a convention (e.g. where developmental processes are seen as irrelevant to evolution), leading to unhelpful divisions between academic fields of enquiry (e.g. the weak link between evolutionary and developmental biology; West-Eberhard, 2003; Amundson, 2005; see Laland et al., 2011, 2013a,b for discussion).

In one sense this screening off of fields of enquiry by researchers might be regarded as inevitable, or perhaps even desirable. To understand a bewilderingly complex and changing world, scientists must devise conceptual tools that render their business more manageable. They assume that, at least for the kinds of questions in which they are interested, with their associated temporal and spatial scales, it is reasonable to treat certain processes, and certain kinds of variation, as relatively unimportant. This allows them to hold certain aspects of the world constant, to treat them as 'context', and to explore the causal structure of the phenomena of interest relative to that context. All scientists do this – although I suspect, few do so deliberately; rather these fundamental assumptions are commonly accepted with little reflection. Accordingly, scientific disciplines effectively become 'clubs' in which like-minded researchers share some consensus over what is, and what is not, reasonably treated as cause and context.

Consider Hutchinson's (1957) famous metaphor of the 'evolutionary play in the ecological theatre'. What does this metaphor imply? To me, it implies that environments are 'out there' – that they are the background, the context, the theater, in which the great evolutionary drama ensues, and where natural selection might perhaps be conceived as the casting director, eliminating or keeping for the next 'showing' a given species of 'actor'. This separation of organism and environment is well-recognized by both biologists and philosophers of biology, and countless researchers have taken issue with it (Barker et al., 2014; Bateson, 1988; Gottlieb, 1992; Keller, 2010; Lewontin, 1983, 2000; Odling-Smee et al., 2003; Oyama, 1985; Oyama et al., 2001). Evolutionary biologists are primarily interested in understanding organismal change and diversity, not ecological change. At the time of the forging of the Modern Synthesis, understanding ecological change was regarded as broadly outside the remit of evolutionary biology – that is ecologists' job (Mayr, 1982). Of course, the last few decades have witnessed the emergence of evolutionary ecology (Ford, 1964; Roughgarden, 1979), whilst the study of eco-evolutionary feedbacks is an exciting recent development (Post and Palkovacs, 2009; Loreau, 2010). Nonetheless, it remains the case today that for the vast majority of evolutionary biologists, the causes of changes in selection pressures are not generally the focus of enquiry, except in some special cases, such as sexual selection. Typically, the selection pressures are taken as the starting point for evolutionary analysis (Endler, 1986a).

Feeding into this division of labor was another longstanding assumption, only recently challenged by evidence for rapid evolution (Kingsolver et al., 2001; Hairston et al., 2005; Ellner et al., 2011), that ecological and evolutionary processes operate of different temporal and spatial scales (Lewontin, 1982, 1983, 2000; Levins and Lewontin, 1985; O'Neill et al., 1986). This assumption was embraced by ecologists and evolutionary biologists alike, in no small part for its convenience (O'Neill et al., 1986). It meant that ecosystem ecologists could disregard evolutionary events as something that likely happened a long time ago, and hence did not need to be considered in their analyses of ecological processes (O'Neill et al., 1986). It also meant that evolutionary biologists could disregard the changes that organisms manifestly brought about in their environments as local and temporary, and hence unlikely to scale up, across populations and over evolutionary timeframes, to be evolutionarily important. One ramification is that evolutionary biologists rarely ask "where do the selection pressures come from?"

The distinction between ecological and evolutionary causes is a scientific convention born through historical accident, rather than from some fundamental truth about how causation operates in the natural world. The forging of the Modern Synthesis in the early part of the 20th century, with its integration of Darwinian natural selection, population-level thinking and Mendelian inheritance, led to the widespread adoption of several core assumptions (Mayr, 1982; Futuyma, 1998). These assumptions included: that new phenotypic variation is a consequence of genetic mutations; that most favorable mutations have small phenotypic effects, which result in gradual phenotypic change; that inheritance is genetic; and that natural selection is the sole explanation for the adaptive match between organisms and their environments. This gene-centric stance led to the view that evolution could appropriately be defined as "a change in the genetic composition of populations" (Dobzhansky, 1937, p. 11), and that it could be studied without reference to mechanisms of development (Mayr, 1982). If evolution is characterized as change in gene frequencies over time, then it is perhaps natural to define evolutionary processes as phenomena that directly bring about changes in gene frequencies. Four such evolutionary processes are widely recognized – selection (natural and sexual), drift, mutation and gene flow – and accordingly they are the only accepted direct causes of evolutionary change.