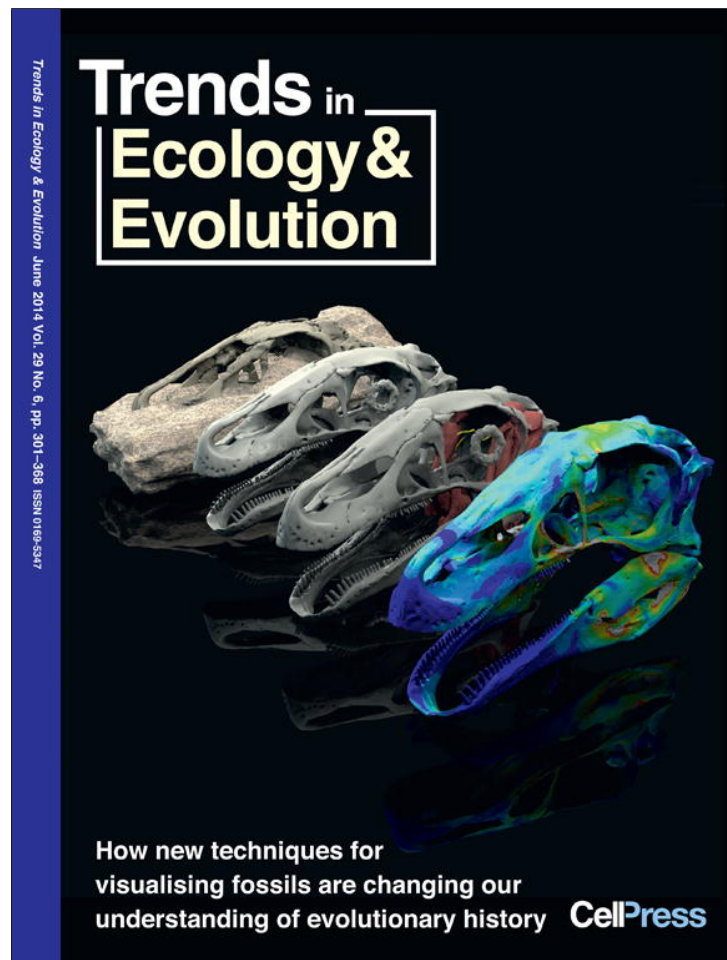


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the climate system and a reduction in the number of simplifying assumptions. The desire to make climate models reflect the complexity of the climate system has stimulated research into the terrestrial carbon cycle, the role of aerosols, and the roles of clouds and ground-to-atmosphere feedback. Would these phenomena have been subjected to such active research without models that required their quantification?

Loneragan offers a counsel of despair: complex models cannot be tested against data unless many data are available. He infers that the search for general patterns across ecology will often be consigned to simple approaches. The result would be stagnation in the progress of ecology. We think that we need to embrace the complexity of the real world and reflect this in our models, and if necessary collect the appropriate data. Thirty years ago Medawar wrote that what 'sets the genuine sciences apart from those that arrogate to themselves the title without really earning it is their predictive capability' ([8], p4). If we think this is

right then we should also wish ecology to be able to make strong predictions: the current focus on simple models is a hindrance in reaching this goal.

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Genetic variation in niche construction: a comment on Saltz and Nuzhdin

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At the beginning of their recent article [1], Saltz and Nuzhdin state that studies of niche construction have paid little attention to the genetic basis of variation in niche-constructing traits. Specifically, they say that 'research has focused on niche-constructing traits that are fixed within populations or species'. However, this statement is only true if one uses a selective definition of niche construction. Niche construction is defined as the changes that organisms make to their environment [2], a definition that Saltz and Nuzhdin concur with [1]. Such changes may be considered 'active' in some way (e.g., choosing a mate, building a nest, defoliating a tree, or mounting an immune response against a pathogen) or be more 'passive' (e.g., defecating, shedding a skin, respiring, or being consumed by saprophytic fungi). For example, pretty much all aspects of animal behaviour are encompassed by niche construction (behavioural responses to the biotic and abiotic environment are pure niche construction, because they in part determine the environment that an animal experiences). However, it would be misleading to suggest that the genetic basis of animal behaviour had not been a topic of tremendous research effort for many years (i.e., not just a recent surge), from the quantitative genetics of behaviour [3] through to increasingly sophisticated molecular biology [4,5]. Similarly, the production of flowers to attract

and manipulate pollinators is again a canonical form of niche construction, yet here too we have an increasing understanding of the genetic basis of flower production, and it would be hard to argue that it had been ignored [6]. More generally, evolutionary and behavioural biologists have in fact amassed a comprehensive knowledge of the genetic basis of variation in many niche-constructing traits across many decades [7], although there is no doubt that many traits remain that we still wish to dissect further. The idea though that such traits are generally viewed as 'fixed' in populations is not tenable.

One possible response to this critique is to use a different, more exclusive definition of niche construction, one that perhaps avoids fields such as life-history evolution, sexual selection, all forms of social behaviour, host–parasite coevolution, and pollination biology. Saltz and Nuzhdin indeed write that they do not think that the role of niche construction theory is to determine what are or are not niche-constructing traits. Yet, surely this can only lead to confusion. If niche construction is to be useful, it must consistently mean something. Only by having a definition that we can work with can we address whether niche construction is really different or new, whether it is a 'neglected process' [2], or whether it is a useful reformulation of existing theories and concepts. Only then can we see whether it brings new insight.

Alternatively, one could respond by saying that only some components of niche construction have been addressed in terms of their genetics. This is undoubtedly true. For

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0169-5347/

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example, there remains the feeling that ecology and evolution continue to be somewhat separate fields, when a more complete synthesis would benefit both. The emergence of fields such as community genetics and eco-evolutionary dynamics certainly attests to ecology and evolution drawing closer in recent times, and a greater focus on genetics in ecology is very much a part of that coming together. In their article [1], Saltz and Nuzhdin focus on niche construction in a developmental context, exploring how genotypes shape phenotypes in part by influencing the environment those phenotypes develop in, and what this means for our understanding of evolutionary genetics. Saltz and Nuzhdin's message is that we do not yet fully appreciate the complexity of the feedback loops between genes and the environment, and I suspect that most readers of *TREE* would be sympathetic to this message. However, by casting this message in terms of niche construction, and in particular the idea that the genetics of niche construction have been neglected, there is the risk of appearing either to misunderstand niche construction, to be selective in the use of the term 'niche construction', or to neglect the work of hundreds of biologists across many subdisciplines.

In fact, true novelty in terms of the genetics of niche construction would probably come from identifying the genetic basis of traits not associated with niche construction. These would be traits that did not influence growth, movement, responses to the environment, feeding, or reproduction. That would truly be a research programme to test the resourcefulness of readers of *TREE*.

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Genetic variation in niche construction and its implications: response to Shuker

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In our recent opinion paper in *TREE* [1], we advanced the idea that genetic variation in niche construction may have understudied consequences for the development and genetics of phenotypically plastic traits, and that these consequences are potentially of evolutionary importance. Our main idea was that alleles underlying genetic variation in niche construction specify the environment in which all traits (and their associated genetic mechanisms) are expressed. Thus, alleles underlying genetic variation in niche constructing traits can have indirect effects on phenotypically plastic traits by influencing the environments that individuals experience.

In a letter written in response to our paper, Shuker [2] raises two key points regarding genetic variation in niche construction. First, Shuker notes that the genetic basis of many niche-constructing traits, especially behaviors, is already a topic of intense investigation. We completely agree, and cite many examples in the paper (e.g., [3,5–10,13,20,23,24,31,34,39,55] in [1]), although of course there are many more. Our point is that implications of such genetic variation for other traits (i.e., for the development, genetics, and evolution of any trait that is phenotypically

plastic) have not yet been widely recognized (see Figures 1 and 2, and Box 3 in [1]). Evidence that these areas of research are neglected can be inferred from the fact that few papers explicitly demonstrate how genetic variation in niche construction influences the development and genetics of phenotypically plastic traits (i.e., through gene–environment correlations and genotype–environment covariation). The near-ubiquity of genetic variation in niche construction that Shuker describes suggests that such effects are widespread and, thus, deserve more empirical and theoretical attention.

Shuker's second set of points relate to the novelty and utility of niche construction as an idea. First, he notes that, 'If niche construction is to be useful, it must consistently mean something' [2]. We define niche construction in the first line of our paper [1]: 'the process in which the traits of an organism determine the environment that it experiences', following the original paper that coined the term [3]. Shuker writes that a clear definition of niche construction is needed to determine 'whether niche construction is really different or new' [2]. Niche construction is not new. The original paper defining niche construction and describing some of its implications was published almost 2 decades ago [3] and drew heavily on existing ideas in ecology, animal behavior, social evolution, and anthropology. Even the controversy over whether niche construction is new and/or useful is, itself, not new (reviewed in [4]).

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0169-5347/

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