COMMENTS



Why Gupta et al.'s critique of niche construction theory is off target

MARCUS W. FELDMAN¹, JOHN ODLING-SMEE² and KEVIN N. LALAND^{3*}

¹Department of Biology, Stanford University, Stanford, USA

²Mansfield College, University of Oxford, Oxford, UK

³ University of St Andrews School of Biology, St Andrews, KY16 9ST, Scotland, UK

*For correspondence. E-mail: knl1@st-andrews.ac.uk.

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Abstract. Gupta *et al.*, in their article in this issue ('Niche construction in evolutionary theory: the construction of an academic niche?'. doi:10.1007/s12041-017-0787-6), lament 'serious problems with the way science is being done' and suggest that 'niche construction theory exemplifies this state of affairs.' However, their aggressively confrontational but superficial critique of niche construction theory (NCT) only contributes to these problems by attacking claims that NCT does not make. This is unfortunate, as their poor scholarship has done a disservice to the evolutionary biology community through propagating misinformation. We correct Gupta *et al.*'s misunderstandings, stressing that NCT does not suggest that the fact that organisms engage in niche construction is neglected, nor does it make strong claims on the basis of its formal theory. Moreover, the treatment of niche construction as an evolutionary process has been highly productive, and is both theoretically and empirically well-validated. We end by reflecting on the potentially deleterious implications of their publication for evolutionary science.

Keywords. niche construction; evolutionary biology.

Gupta *et al.* (2017) take issue with three alleged claims of niche construction theory (NCT), summing up their concerns as:

'The proponents of NCT make a few claims repeatedly: (i) NC and ecological inheritance have been neglected; (ii) there is a vast body of formal theory on NC and its ecological and evolutionary consequences that is a significant addition to SET; and (iii) NC and, more recently, NC/developmental bias are important evolutionary processes at par with natural selection in the context of explaining adaptive evolution.'

In fact, NCT does not make the first two of these claims, while the third is a perfectly legitimate scientific position that has proven productive across multiple academic fields, and is stimulating ongoing empirical and theoretical research.

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Niche construction theory does 'not' claim that niche construction and ecological inheritance are neglected. It is unfortunate that Gupta et al. should waste so much of their own and other's time attacking positions that NCT does not take. NCT has never made the claim that the fact that organisms engage in niche construction is neglectednot once, let alone repeatedly-as is apparent to those that have read our book and papers carefully. Gupta et al. provide no quotes to justify this assertion. We can only surmise that their confusion derives from the subtitle of our monograph 'Niche construction: the neglected process in evolution' (Odling-Smee et al. 2003), the correct reading of which is that, whereas niche construction has been widely studied as a phenomenon, it has not been widely recognized as an evolutionary process. Clearly, Gupta et al. dispute that niche construction should be recognized as an evolutionary process; however, that it is not formally listed as a cause of evolution in virtually all evolutionary literature is incontestably true. This means there is no false claim on our part, but rather a false attribution on their part: Gupta et al. wrongly believe that NCT claims the phenomenon of niche construction has been neglected.

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That Gupta *et al.* should make this error, when even the most cursory glance at our monograph (Odling-Smee et al. 2003) reveals an extensive review of previous empirical findings and past theory, suggests serious shortcomings in their scholarship. The review of previous empirical findings is 65 pages long, with detailed tables that document many hundreds of empirical examples dating back to the 19th century (Odling-Smee et al. 2003, pp. 50-115). It would not be unreasonable to characterize this literature review as 'encyclopaedic', and it remains widely used as a source. The review of past theory covers evolutionary models of frequency and density dependent selection, habitat selection, coevolution, maternal effects, epistasis and indirect genetic effects, ecological and demographic models of resource depletion, and includes several quantitative genetics analyses (Odling-Smee et al. 2003, pp. 116–133). If the meaning of the subtitle of our book had been ambiguous prior to reading the book, it would certainly not be afterwards. Nor would such a reading support Gupta et al.'s slur that NCT does not appropriately acknowledge the contributions of earlier researchers. It is particularly troubling, however, that Gupta et al. cite an article (Scott-Phillips et al. 2014) that clarifies this issue explicitly, and yet still make their erroneous attribution. Either Gupta et al. are guilty of not reading the material they review, which would be disturbing enough given the derogatory tone they use, or they have deliberately chosen to attack claims that they know have not been made.

Niche construction theory does 'not' make strong claims on the basis of its formal theory. If the first issue is a red herring, the second is just plain silly. To our knowledge, no article written by NCT researchers has ever claimed it has generated 'a vast body of formal theory' or suggested that its models supersede other theory. This is Gupta et al.'s exaggeration not ours. The strongest claim we make is: 'An extensive body of formal theory explores the evolutionary consequences of niche construction and its ramifications for evolutionary biology and ecology' (Laland et al. 2016). Restricting attention to those studies that explicitly cite and draw on NCT, we estimate that the mathematical NCT literature amounts to about 30-40 published papers. Hence, the legitimacy of Gupta et al.'s complaint revolves around whether it is appropriate to apply the adjective 'extensive' to 30-40 articles. While we suspect that most readers would not find this use of language inappropriate, it is an entirely subjective judgment. Asking how big a literature should be before a particular word is appropriate is like asking how long is a piece of string. Obviously, NCT constitutes only a tiny part of theoretical biology. But that is irrelevant, as no one has claimed that NCT is comparable to, incompatible with, or supersedes, other bodies of theory, and Gupta et al. are wrong to imply that the case for an extended synthesis rests on this work. Of course, there is previous theory. Yet, as we write in our book (pp. 132), 'while many

separate theoretical domains investigate phenomena with features in common with niche construction, none of these captures all the pertinent characteristics'. We agree that theory derived for other purposes sheds some light on niche construction, but it is no substitute for dedicated theory specifically designed to address relevant evolutionary issues.

Gupta et al. denigrate the NCT literature, claiming its findings are 'neither surprising nor unexpected'. Formal models of niche construction deploy standard population genetic and ecological methods; thus it should be neither a surprise nor a problem that some of the findings could be anticipated given the existing literature. Of course, it is easy to claim retrospectively that a scientific finding is obvious. The novelty or value of this literature is no less a subjective evaluation than the number of articles it takes to make up a significant body. Nevertheless, these articles on NCT were of sufficient novelty and produced sufficient new insight to merit publication in prestigious and wellrespected journals such as PNAS, Evolution, American Naturalist, Journal of Evolutionary Biology and Theoretical Population Biology. We are comfortable that these papers represent an extensive and significant contribution.

Niche construction as evolutionary process. Lewontin (1982, 1983, 2000) argued that conventional evolutionary treatments downplay the active role of the organism in evolution. He drew attention to how organisms modify natural selection by altering environments, determining what is relevant, transducing signals and creating novel statistical patterns in resources. These and other conceptual innovations led to the claim (Odling-Smee et al. 2003), that niche construction acts to bias natural selection along particular trajectories by reliably and consistently influencing environmental states (i.e., that niche construction is an evolutionary process). Some people find Lewontin's arguments compelling; others do not. NCT takes a currently heterodox position vis-à-vis evolutionary theory. But there is nothing wrong with that. Scientific ideas should be judged on the basis of their ability to advance empirical and theoretical research. Alternative perspectives are of value precisely because they inspire generation and testing of novel hypotheses, and opening new lines of enquiry. Niche construction theory has done exactly that in both biological and social science.

Mathematical papers represent a small fraction of the rapidly growing literature on niche construction, which now includes over a thousand articles and several books. Most of these studies use NCT in other productive ways, to inspire empirical research and shed new evolutionary light on diverse topics, ranging from the Cambrian explosion (Erwin and Valentine 2013), to human evolution (Fuentes 2009; Kendal *et al.* 2011), to evolutionary ecology (Sultan 2015), to the origin of language (Bickerton 2009), or the advent of agriculture (Smith 2007; Zeder 2015). The repeated invocation of NCT's claims in part

reflects its application in many different academic fields as researchers discover the framework and apply it to their own problems. That hundreds, perhaps thousands, of researchers spanning diverse disciplines find NCT interesting and useful, and believe NCT produces important insights, certainly argues that NCT is valuable science and not, as Gupta *et al.* claim, 'incessant repetition of largely untenable claims'. What attracts people to NCT is primarily Lewontin's emphasis on the active agency of the organism, which resonates with their own assessments of the role that agents play in their focal science. NCT does not stand or fall on its formal theory: if there were none it would still be making a valuable contribution. It should be judged on whether it is useful to place emphasis on organismal agency in evolution.

What does Gupta et al.'s paper teach us about evolutionary science? Gupta et al. rudely characterize NCT researchers as 'muddled' or deploying 'rhetorical devices', without checking whether their understanding of the work they criticize is correct. The combination of their egregious claims and poor scholarship has led to the extensive propagation of misinformation about NCT and to confusion as to what niche construction and its theory actually are. This episode was unnecessary: Gupta et al. could-and perhaps should-have approached us with their concerns, and we would have attempted to correct their misunderstandings. If differences remained, we could have worked together to present these in a constructive form that would have drawn attention to unsolved problems and potential future research avenues. This constructive approach has been taken before, and leads to a much more informed and productive scientific dialogue (Scott-Phillips et al. 2014; see also Uller and Helanterä 2017).

NCT has constructed a conceptual niche for itself, but Gupta et al. are wrong to imply that there is anything sinister or unusual about this. All new theories develop conceptual niches, by generating ideas, insights and methods that might inspire others to use them. In fact, successful theories typically construct two niches, the second being the creation of opportunities for others to make a name for themselves by attacking the theory. That Gupta et al.'s treatment is riddled with inaccuracies, together with their aggressive promotion of their article even prior to publication, will lead many readers to draw the conclusion that Gupta et al. have sought to make their reputations by 'bringing down' NCT. Whatever their motives, Gupta et al.'s critique is badly off target. We are grateful to the editor of this journal for giving us the opportunity to respond, even though Gupta et al.'s paper should never have been published.

Many established theories start off as heresy; without innovation there can be no progress. All scholars have every right, or even an obligation, to think differently from the mainstream, and if they do, to try to convince others of their merits of their work. The most dangerous aspect of Gupta *et al.*'s article is its criticism of 'an increasing trend of setting up one's work as a competing counterpoint to some dominant idea in the field, even if the work is actually complementary to that dominant idea'. This is dangerous because empirical and theoretical discoveries can always be derogated as being in line with the dominant conceptual line; this privileges established theory. Rather than warning against this, we value evolutionary research that provides a 'competing counterpoint'. In going against the mainstream, we encourage researchers to lay out their reasoning and assumptions clearly, highlighting conceptual differences so that these can be subject to empirical assessment, and to repeat their claims as many times as they feel necessary. Evolutionary biologists should not be intimidated into falling in line with the majority, but should feel free to express their ideas in whatever way they deem most useful. We also encourage researchers to be wary of superficial critiques that fail to engage with the conceptual issues. Pluralism of perspective is absolutely critical to the institution of science: rather than being subject to Gupta et al.'s derogatory and polemical assessment of new scientific ideas as 'post truth', such innovations may eventually become part of the mainstream.

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