of immigration and extinction are indeed to be expected under some circumstances. Secondly, they demonstrate that a combination of metapopulation theory and evolutionary theory can be useful in analyzing how biodiversity transients depend on the characteristics of both the ecosystem and the forcing factor. This can help to identify the rage of circumstances under which deficits and surpluses might arise.

JS rightly state that integration of delayed extinction and immigration is needed to understand biodiversity dynamics. I hope to have demonstrated that such integration indeed yields useful new insights.

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Letters Response

Response to 'Biodiversity "surpluses" and "deficits" are not novel issues': We agree

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Extinction and immigration events set in motion by environmental change can take a long time to play out, leading to transient extinction debts and immigration credits for particular communities, landscapes or regions [1]. When we prepared our article discussing these phenomena [1], we were unaware of Dr. Nagelkerke's book chapter [2], and regret our oversight. As Dr. Nagelkerke points out in his commentary, that chapter develops a concept of colonization credit that is parallel to our concept of immigration credit. Its formal analysis [2], based on metapopulation theory, is an important contribution to the goal of understanding transient biodiversity dynamics. We believe that transient dynamics needs to be addressed from a variety of perspectives, including metapopulations embedded in landscapes, but also at broader biogeographic scales, and employing both theoretical and empirical approaches. Immigration and extirpation rates are controlled by a wide array of processes operating across a broad range of temporal and spatial scales. The metapopulation approach is an important one, and the chapter [2] should be consulted by any reader interested in the topic. We also draw attention to a recent paper aimed at broader timescales [3], in which evolutionary 'diversification debt' bears analogies with our 'immigration credit'.

We confess embarrassment at our oversight, which in our experience is becoming an increasingly frequent phenomenon. This is not the first time we have learned of an important and relevant paper we should have cited in one of our publications, and of course we are disappointed on the various occasions when our own hard-won contributions get overlooked by others. It seems that ecologists are faced with a 'sorcerer's apprentice' problem[1]. The increasing success and relevance of ecology has led to rapid proliferation of ecological literature, with more (and bigger) journals and books to keep track of. The problem is compounded as ecology becomes increasingly interdisciplinary, requiring that we keep up with other rapidly expanding literatures. No master sorcerer appears to be waiting in the wings to break the spell, but we retain hope that more efficient ways to manage the information flood will emerge.

In the meantime, we repeat our appeal for ecumenical, interdisciplinary efforts to assess and mitigate the multiple threats to biodiversity [1,4]. Transient dynamics with time-lags are little studied, yet are likely to prevail in a changing world. For example, biodiversity deficit within an ecosystem owing to rapid extirpation and delayed immigration may result in weakened ecosystem function and reduced ecosystem services for decades to centuries. Conversely, biodiversity surplus resulting from a climate-driven immigration pulse may mask eventual biodiversity decline as incumbent species undergo delayed extinction. Understanding these dynamics, both theoretically and empirically, is an urgent priority if ecologists are to provide useful advice to policymakers and resource managers.

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[1] We refer here to the problem as originally delineated by the anonymous protagonist of Goethe's 1797 poem, *Der Zauberlehrling*, and later experienced by Mickey Mouse in Disney's 1940 film, *Fantasia*.

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Book Review

Artifacts of the evolving mind: what tool use tells us about early human cognition

Stone Tools and the Evolution of Human Cognition edited by April Nowell and Iain Davidson. University Press of Colorado, 2010. $65.00 hbk (234 pages). ISBN 978 1 60732 030 2.

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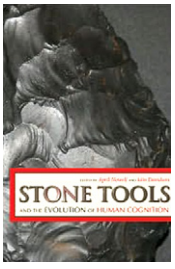

Modern human beings are unique both in their cognitive style and in their reliance upon complex technology to sustain their way of life; and there can be no doubt that it is our ability to reason symbolically that underwrites our familiar ability to dream up and (thanks to our dexterity) to make ever more complex tools. But it was not ever thus. Both our recent technologies and our symbolic consciousness clearly emerged from much simpler precursor states. The archaeological record begins with the appearance of the first simple stone tools some 2.5 million years ago, at a time when our hominid precursors still had essentially ape-sized brains and small, archaically-proportioned bodies. Between then and the end of the last Ice Age, some 12 000 years ago, Old Stone Age technologies became incrementally more complex (with vast spans of time typically elapsing between major innovations); and, slightly later, metabolically-expensive hominid brains began to expand (in a pattern poorly understood in detail, but that nonetheless shows a strong time-related trend towards greater size). Stone tools are, of course, the archaeologist's dream: they are the most durable of all products of human behavior, and have left an incomparable record. In frustratingly stark contrast, cognition is the most intangible of features and leaves no direct imprint: its qualities have to be guessed from physical proxies, among which brain size is sadly and notoriously imponderable.

Little wonder, then, that increasing numbers of archaeologists, linguisticians, cognitive scientists and others have been asking exactly what we might be able to infer about the evolution of the elusive but vital quality of hominid cognition from the extensive and durable stone tool record. Uniting as it does so many realms of expertise, the resulting field of research (one might call it 'palaeocognition') came of age in 1993 with the publication of a landmark conference volume edited by Kathy Gibson and Tim Ingold [1]. Now, the anthropologist April Nowell and the archaeologist Iain Davidson have edited a worthy, if perhaps inevitably more selective, successor volume.

Stone Tools and the Evolution of Human Cognition brings together nine chapters by well-known authors who focus on stone tools from a variety of perspectives, and in a broadly chronological sequence. Mark Moore sets a rather abstract conceptual scene by relating knapping 'design space' to the 'grammars of action' obtained from ordering motor actions. Ignacio de la Torre concludes that the early 'Oldowan' stone tool kits reflect an 'exponential qualitative leap' in technical competence over anything done by non-hominid toolmakers. April Nowell and Mark White rather uneasily suggest that the typological stasis of the following Acheulean industry might have concealed more variety in other aspects of the makers' lives. Thomas Wynn and Frederick Coolidge look at Middle Paleolithic technology and plausibly propose that the high technological expertise involved is decoupled from language and symbolism. Focusing on the Lower and Middle Paleolithic, Steven Kuhn looks at the difficulties inherent in categorizing of stone tools and urges wider use of quantitative approaches. Sarah Wurz examines the Middle Stone Age lithics from the classic South African sites of Klasies River Mouth, expressing judicious reservations as to whether the varying traditions preserved at the locality between about 120 and 60 thousand years ago (or indeed elsewhere in the MSA of South Africa) reflect symbolic thought. Dietrich Stout reviews brain-imaging studies, and concludes that circuits involved early on in stone-knapping might later have been co-opted for speech. Iain Davidson argues from several different lines of evidence that stone tools are indeed a useful repository of information about the cognitive status of their makers, but that interpretation of the evidence is currently constrained by inadequate

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