

As described in detail elsewhere [3], Charles Lyell, writing in the first half of the 19th century, listed biotic homogenization (along with habitat destruction and hunting) as one of the main mechanisms by which human activities were leading to widespread extinctions. In particular, he pointed out that many animals that had been domesticated by humans were now found in large numbers on continents such as America and Australia, where they had previously been absent. He wrote that ‘The fact that so many millions of wild and tame individuals of our domestic species, almost all of them the largest quadrupeds and birds, having been propagated throughout the new continent within the short period that has elapsed since the discovery of America... affords abundant evidence of the extraordinary changes which accompany the diffusion and progressive advancement of the human race over the globe’ [4]. Interestingly, Lyell uses this as an argument in favour of the recent origin of humans, his idea being that, if we had a long geological history, this homogenization would be already complete.

As previously described [3], one of the most surprising aspects of Lyell’s discussion to a modern reader is that he

does not consider the resulting extinctions to be a cause for concern. Indeed, he considers human-caused extinctions to be a natural process, pointing out that any expanding species must lead to the reduction or extinction of other species. He considered that this applied as much to humans as to ‘the lion, when it first spread itself over the tropical regions of Africa’ [4], although he conceded that not all of his contemporaries held such a relaxed view of these changes. However, he cited poets, rather than ‘scientists’, as the people who lamented these changes.

References

- 1 Olden, J.D. *et al.* (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* 19, 18–24
- 2 Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*, Methuen and Co
- 3 Wilkinson, D.M. (2002) Ecology before ecology: biogeography and ecology in Lyell’s ‘Principles’. *J. Biogeogr.* 29, 1109–1115
- 4 Lyell, C. (1832) *Principles of Geology* (Vol. 2), John Murray

0169-5347/\$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.tree.2004.03.025

Letter Response

Clarifying biotic homogenization

Julian D. Olden and N. LeRoy Poff

Department of Biology, Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA

David Wilkinson correctly points out [1] that Charles Lyell’s recognition of species invasions and extinctions pre-dates the writings of Charles Elton by a century. Although we acknowledge the historical interest of this fact, we consider the assertion that the process of biotic homogenization is synonymous with widespread invasions and extinctions to be incorrect. Therefore, Lyell was not commenting about biotic homogenization as it is contemporaneously used. Here, we take the opportunity to clarify the subtlety of the concept of biotic homogenization.

Biotic homogenization basically refers to an increase in species similarity in space over time, and it can arise through several ecological mechanisms. Ecological processes leading to homogenization represent specific, and often quite different, interactions among non-native species, native species, and the environment ([2], Figure 2 in [3], Figure 1 in [4]), and they need not include either species invasion or extinction [4]. Rather, the degree of homogenization crucially depends on the taxonomic identities (and functional roles) of the species in the community, as well as on the rate and spatial pattern at which species are gained and lost across the landscape. Indeed, as recently illustrated [4,5], biotic homogenization can arise when only species invasions occur without any commensurate species extinction. The converse can also lead to homogenization. Furthermore, and significantly,

species invasions and extinctions (whether individually or interactively) can promote the opposite of biotic homogenization by causing regions to become more dissimilar in their species composition (referred to as ‘biotic differentiation’ [4]).

In conclusion, our research and that of others (e.g. [6–8]) shows that, although species invasions and extinctions do often fuel biotic homogenization (and differentiation), the details of temporal and spatial patterns at which these events are occurring provide the subtle context in which the homogenization process operates. The insufficiency of invasion and extinction alone to describe biotic homogenization leads us to argue that this process should be considered a unique ecological phenomenon [9], one first recognized by Charles Elton in his insightful treatise [10].

References

- 1 Wilkinson, D.M. (2004) The long history of homogenization. *Trends Ecol. Evol.* 19, 282–283
- 2 McKinney, M.L. and Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14, 450–453
- 3 Rahel, F.J. (2002) Homogenization of freshwater faunas. *Annu. Rev. Ecol. Syst.* 33, 291–315
- 4 Olden, J.D. and Poff, N.L. (2003) Toward a mechanistic understanding and prediction of biotic homogenization. *Am. Nat.* 162, 442–460
- 5 Olden, J.D. and Poff, N.L. (2004) Ecological mechanisms driving biotic

Corresponding author: Julian D. Olden (olden@lamar.colostate.edu).

- homogenization – testing of a mechanistic model using fish faunas. *Ecology* (in press)
- 6 Rahel, F.J. (2000) Homogenization of fish faunas across the United States. *Science* 288, 854–856
- 7 Marchetti, M.P. *et al.* (2001) Homogenization of California's fish fauna through abiotic change. In *Biotic Homogenization* (Lockwood, J.L. and McKinney, M.L., eds), pp. 259–278, Kluwer Academic/Plenum Publishers
- 8 Taylor, E.B. (2004) An analysis of homogenization and differentiation

- of Canadian freshwater fish faunas with an emphasis on British Columbia. *Can. J. Fisheries Aquat. Sci.* 61, 68–79
- 9 Olden, J.D. *et al.* (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* 19, 18–24
- 10 Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*, Methuen

0169-5347/\$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.tree.2004.03.024

Book Reviews

A mania for modules

Modularity in Development and Evolution by Gerhard Schlosser and Günter P. Wagner. Chicago University Press, 2004. £63.00/£24.50 hbk/pbk (600 pages) ISBN 0226738531/0226738558

Armand M. Leroi

Department of Biological Sciences, Imperial College London, Silwood Park Campus, Ascot, Berkshire, UK, SL5 7PY



Abstract nouns – ‘hierarchy’, ‘connectivity’, ‘evolvability’, ‘complexity’ to name four – are becoming increasingly popular as evolutionary developmental biology tries to find its theoretical feet. With Gerhard Schlosser, an amphibian developmental biologist, Günter Wagner has brought together a stellar team of contributors to discuss the

abstract noun *du jour*, ‘modularity.’

In *Modularity in Development and Evolution*, we can read contributions from 42 authors, many of them distinguished, about topics as diverse as basic helix–loop–helix transcription factors, data-mining genome-wide expression data, vertebrate limbs, nematode vulvas and *Wolbachia* symbionts. Unsurprisingly, all authors agree that modularity is very important to development. The question is: what do they mean?

The answer is: many different things. The editors make a brave attempt to keep matters under control by defining modules as structures or processes composed of tightly integrated parts, whilst being relatively autonomous from their surroundings. For developmental geneticists, modules are therefore groups of proteins that work together to specify cells [e.g. the Notch–Delta–Su(H) pathway]. For a quantitative geneticist, modules can be seen in the distribution of the pleiotropic effects of quantitative trait loci, which control various morphological traits. Developmental neurobiologists point to embryologically and functionally distinct units of the central nervous system, whereas a nematode geneticist points to cells. Bioinformaticists see modules in ‘synexpression groups’ – clusters of co-ordinately regulated genes visible from expression profiling studies; dynamic systems modelers see them as networks of genes necessary and sufficient for carrying out a particular function; a complexity theorist sees them in basins of attraction in random boolean networks. And this is only a partial list.

The sheer ubiquity of modular things, whatever those happen to be, suggests that modules matter to development. Having said that, one has the feeling that many contributors

are cherry-picking the data. They are looking for, and finding, modules whilst ignoring non-modules. The problem seems to be that the modularity of things is, as the editors point out, a matter of degree. However, there is no formal theory of modularity and, in the absence of that, no consensus about how to measure it. The result is that we are invariably given the history of a case rather than a sense of its distribution. This is a natural history of modules.

What about their evolution? As with more mundane attributes that organisms might have, say, parental care or wings, evolutionary biologists want to know several things about them. Why do modules exist? Are they the result of natural selection? Or can mutation and drift explain their presence? If selection, what kind of selection? We also want to know how they evolve. If a module is found in *Caenorhabditis elegans*, is it also found in another nematode species? A fruit-fly? Humans? Are modules more conserved than non-modules? Has modularity – like complexity – increased over the course of evolution?

These are important but difficult questions, and the contributors give a diversity of answers. Taking the last set of questions first, (how do modules evolve), it seems that sophisticated comparative studies of the evolution of modules are some way off. This is not a criticism: such studies need lots of data, which hardly exist outside of a few model organisms – but they will surely come. Why do modules exist? Some contributors seem to view modularity as an emergent property of genetic networks. Others suggest that developmental modularity evolves for its variational properties – it enables organisms to be more resistant to environmental or mutational perturbations. The split here is analogous to the Wright–Fisher dispute over dominance. Others again, suggest that modules permit evolvability (i.e. the production of heritable, selectable, phenotypic variation). This is a clade-selection argument – with all the weaknesses of such arguments. Many contributors hedge their bets by citing some or all of the above without considering the matter too deeply. But more careful discussions can be found in at least two papers. Force, Cresko and Pickett argue that ‘genotypic modularity’ – the use of genes in particular places and times independently of other genes – can increase simply as a consequence of

Corresponding author: Armand M. Leroi (a.leroi@ic.ac.uk).