**References**
1 Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, Clarendon Press
2 Endler, J.A. (1986) *Natural Selection in the Wild*, Princeton University Press
3 Felsenstein, J. (1985) Phylogenies and the comparative method. *Am. Nat.* 125, 1–15
4 MacColl, A.D.C. (2011) The ecological causes of evolution. *Trends Ecol. Evol.* 26, 514–522
5 White, C.R. *et al.* (2007) Basal metabolic rate of birds is associated with habitat temperature and precipitation, not primary productivity. *Proc. R. Soc. B* 274, 287–293
6 Arnold, S.J. *et al.* (2008) Understanding the evolution and stability of the G-matrix. *Evolution* 62, 2451–2461
7 Odling-Smee, F.J. *et al.* (1996) Niche construction. *Am. Nat.* 147, 641–648
8 Wolf, J.B. *et al.* (1998) Evolutionary consequences of indirect genetic effects. *Trends Ecol. Evol.* 13, 64–69
9 Moya-Laraño, J. (2010) Can temperature and water availability contribute to the maintenance of latitudinal diversity by increasing the rate of biotic interactions? *Open Ecol. J.* 3, 1–13
10 Moya-Laraño, J. (2011) Genetic variation, predator-prey interactions and food web structure. *Philos. Trans. R. Soc B* 366, 1425–1437
11 Thompson, J.N. (2005) *The Geographic Mosaic of Coevolution*, University of Chicago Press
12 Moya-Laraño, J. and Wise, D.H. (2007) Direct and indirect effects of ants on a forest-floor food web. *Ecology* 88, 1454–1465


doi:10.1016/j.tree.2011.11.013 Trends in Ecology and Evolution, March 2012, Vol. 27, No. 3

# The story of O: reply to Moya-Laraño

**Andrew D.C. MacColl**

School of Biology, University of Nottingham, University Park, Nottingham, NG7 2RD

In my recent review in *TREE* of the ecological causes of evolution [1], I used the term 'O matrix' to describe the variance–covariance matrix that quantifies variation in, and spatiotemporal correlations between, those elements of the environment, selective agents, that cause the association between fitness and phenotype that is called 'natural selection'. Similar structure in the environment has long been recognised by ecologists in the spatial correlations between, for example, competition, predation and abiotic factors, that make it difficult to discern the environmental causes of the distributions of species [2–4]. However, the consequences of this structure for the process of natural selection have seldom been recognised or taken into account by evolutionary biologists.

In his interesting letter, Moya-Laraño [5] makes three points about the O matrix. The first is that the O matrix has been implicitly used in comparative analyses. This is true in a limited sense. Limited, because (i) analyses that have simultaneously examined the associations between adaptations and multiple environmental variables are unusual; and (ii) such analyses are retrospective and, therefore, run the risk of confounding the true cause of selection (and evolution) with factors that operate at an ecological level, such as plastic responses to the environment and habitat choice.

The second is that the O matrix needs to be stable. Environments vary spatially and fluctuate temporally, and it is exactly these variations that the O matrix describes. The utility of the O matrix as a concept depends not on whether the environment is stable (it is not), but on the extent to which different aspects of the environment covary in space and time. If correlations between selective agents remain similar (e.g. predation high where competition is high, or low where it is low [2]), throughout the distribution or evolutionary history of species, then O matrices are stable. The extent to which this is true is an empirical question that can only be revealed by research, but the ecological literature [3,4] suggests that O matrices are likely at least to be spatially stable.

The third point is that, in addition to the O matrix affecting the evolution of organisms and structure of correlations between traits (the 'G' matrix), as I suggested [1], the G matrix in turn may reciprocally affect O matrices. This is true, and an emerging theme of recent eco-evolutionary research is that organisms can shape their environments [6,7]. However, although organisms are often shaped by their environment, the effect of the organism on the environment is necessarily more diffuse: most organisms are unlikely to affect the basic physicochemical properties of the environment [8], let alone climate fluctuations such El Niño [9] or the North Atlantic Oscillation [10]. Even for humans, it seems unlikely that the exact shape of the G matrix matters very much in this regard!

**References**
1 MacColl, A.D.C. (2011) The ecological causes of evolution. *Trends Ecol. Evol.* 26, 514–522
2 Connell, J.H. (1961) Influence of interspecific competition and other factors on distribution of barnacle *Chthamalus stellatus*. *Ecology* 42, 710–723
3 Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology* 84, 2809–2815
4 Gaston, K.J. (2003) *The Structure and Dynamics of Geographic Ranges*, Oxford University Press
5 Moya-Laraño, J. (2012) O-matrices and eco-evolutionary dynamics. *Trends Ecol. Evol.* 27, 139–140
6 Harmon, L.J. *et al.* (2009) Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* 458, 1167–1170
7 Post, D.M. and Palkovacs, E.P. (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philos. Trans. R. Soc. B* 364, 1629–1640
8 White, C.R. *et al.* (2007) Basal metabolic rate of birds is associated with habitat temperature and precipitation, not primary productivity. *Proc. R. Soc. B* 274, 287–293
9 Gibbs, H.L. and Grant, P.R. (1987) Oscillating selection on Darwin's finches. *Nature* 327, 511–513
10 Garant, D. *et al.* (2004) Climatic and temporal effects on the expression of secondary sexual characters: genetic and environmental components. *Evolution* 58, 634–644

*Corresponding author:* MacColl, A.D.C. (andrew.maccoll@nottingham.ac.uk).


doi:10.1016/j.tree.2011.11.012 Trends in Ecology and Evolution, March 2012, Vol. 27, No. 3