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## **O-matrices and eco-evolutionary dynamics**

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Jordi Moya-Laraño

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Functional and Evolutionary Ecology, Estación Experimental de Zonas Áridas, EEZA-

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CSIC, Carretera de Sacramento s/n, 04120-Almería, Spain

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email: [jordi@eeza.csic.es](mailto:jordi@eeza.csic.es)

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18 “Natural selection is not evolution” [1]. This simple statement explains how we pursue  
19 the study of natural selection, as it separates within-generation natural selection from  
20 the multiple-generation evolutionary response to natural selection. Actually, we can  
21 estimate natural selection by just measuring the relevant traits of organisms during a  
22 single growing and breeding season [2]. However, a good understanding of adaptive  
23 evolution cannot be achieved without considering the selective agents responsible for  
24 natural selection. The comparative method in evolutionary biology [3] was born in part  
25 to fill this gap, serving very successfully since then to document how selective agents  
26 drive adaptive variation at scales that expand from a few to millions of generations.  
27 However, the systematic inclusion of selective agents in studies documenting natural  
28 selection in the wild has been much less common.

29         In a recent review in TREE, MacColl [4] proposes a new research programme  
30 that aims at measuring and manipulating selective agents in field studies of natural  
31 selection. Making selective agents come to the surface may be a major step forward in  
32 evolutionary biology. MacColl has done an excellent job at envisaging how research in  
33 this area should be pursued. Using the analogy with variance-covariance genetic  
34 matrices (G-matrices) of quantitative characters, he proposes the use of variance-  
35 covariance O (*Oikos*) matrices of selective agents and to relate them to the strength of  
36 selection [2] by means of multiple regression. Actually, O-matrices have been implicitly  
37 used in the comparative method, as the most modern statistical techniques allow for the  
38 test of partial and interaction effects of candidate selective agents on trait values [e.g. 5].  
39 Since, in order to detect their role in adaptive evolution through the comparative  
40 method, selective agents should be present and relatively constant through a great part  
41 of the evolutionary history of the focal taxon, these are stable O-matrices in the

42 MacColl's sense. However, at the temporal scales at which selection is measured in the  
43 wild, these O-matrices may not be always as stable.

44         If spatio-temporal fluctuation in climatic factors (rainfall, temperature), and the  
45 associated productivity, is sufficiently high at temporal scales shorter than the average  
46 lifespan of individuals in the target population, selection may be undetectable.  
47 Furthermore, abundances of interacting populations may fluctuate enormously in space  
48 and time regardless of climate variability. Thus, even in relatively stable ecosystems,  
49 the O-matrix may fluctuate sufficiently to produce noisy patterns of selection. When  
50 feasible, experimental manipulations may partially solve this problem [4]. In non-  
51 manipulative studies, one could check if environmental fluctuations affect selection by  
52 testing for an interaction effect between agent fluctuation and trait values on fitness.

53         Moreover, if O-matrices affect the evolution of G-matrices (i.e., over many  
54 generations the selective environment affects the genetics of trait variation and  
55 correlation – [4]) we must consider that G-matrices, which are relatively stable [6], may  
56 also reciprocally affect O-matrices. This important fact, which may completely change  
57 how we see eco-evolutionary landscapes, was not considered by MacColl. First,  
58 ecosystem engineers can contribute to enhance their own environment by niche  
59 construction, adaptively changing their O-matrices from generation to generation [7].  
60 Second, Indirect Genetic Effects; i.e. the effect of gene expression in one individual on  
61 the gene expression of another, can actually drive the evolution of the biotic  
62 environment itself [8], making the G-matrix to behave in part as the O-matrix and  
63 *viceversa*. Third, if we consider ecological networks as the biotic O-matrices of target  
64 interacting species, the paucity of positive, negative, direct and indirect effects in these  
65 complex systems provides ample room for the O-matrix to affect the G-matrix [9] and  
66 *viceversa*. Actually, variation in the G-matrix can potentially affect variation in the

67 stability of complex food webs [10], and thus the stability of the O-matrix itself.  
68 Furthermore, asymmetric co-selection between pairs of interacting species can  
69 differently affect the demography of each other [11]. Using MacColl's Fig. 1, a change  
70 in the G-matrix due to a response to selection for predatory defence in sites of high  
71 predator density, could affect the density of predators itself, and thus the O-matrix.  
72 Moreover, if the correlation between predator and parasite abundances is driven by  
73 predator density, a decrease in predator numbers will change parasite abundance.  
74 However, if the correlation is mediated by a third variable (e.g.; overall system  
75 productivity) the change in predator numbers will not affect the parasite axis of the O-  
76 matrix. The possibilities may be astronomical when complex networks of interactions  
77 are considered as O-matrices.

78         In order to tentatively explore this feedback among G- and O-matrices, one  
79 could measure O-matrices before and after selection and relate the change in the O-  
80 matrices to the variance-covariance matrix of phenotypic trait values as measured  
81 before selection. To this end, one could use Path Analysis, which is a very useful  
82 statistical tool to disentangle cause and effect when combining experiments and  
83 complex biotic interactions [e.g. 12].

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