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Geobiology of the Critical Zone: the Hierarchies of Process, Form and Life provide an Integrated Ontology

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In the framework of Earth System Science, landscapes are the templates structuring the biosphere: the membranes interfacing between exosphere and geosphere. The hosts of earth surface processes, in their dynamics and complexity, landscapes hold a pivotal position in the evolving earth system – not least in their archives of Earth history. Their landforms document impacts of formative events originating in extra-terrestrial, geological and climatic processes. Nevertheless, major challenges to reconstruct dynamics at this interface between geosphere and exosphere hamper research efforts. Events at the mesoscale over evolutionary timescales are an important reason for why the academic schools of mega- versus process geomorphology persist (see Summerfield MA 2005. Trans. Inst. Brit Geogr NS, 30, 402–415). Austere limits on what their respective methods can reveal in mesoscale phenomena face several problems (besides costs of sampling and analyses). One, surviving landforms often lack the requisite minerals (e.g. of volcanic events). Second, the spatial resolution of orthodox methods (e.g. thermochronology) cannot resolve mesoscale patterns. Third, the surface dating tools with superb spatial precision have finitee temporal limits (Luminescence-Dating and Cosmogenic Isotopes). Fourth, and by no means least, the cumulative impact of earth surface processes has overwritten and/or eroded physical evidence of earlier formative events. (This problem is exemplified in tropical landscapes where deep, pervasive bioturbation is the dominant earth surface process!) The cumulative outcome of these inherent turnovers of landscapes has shaped the inherent emptiness of the Rock Record, which sets absolute limits on its archives (Ager D 1993. The Nature of the Stratigraphical Record; Miall AD 2015. in: Strata and Time: Probing the Gaps in Our Understanding. Geological Society, London, Special Publications, 404, http://dx.doi.org/10.1144/SP404.4).

These limitations on mesoscale geomorphology characterize Africa's older surfaces, many of which qualify as palimpsests: overwritten and reshaped repeatedly over timescales of 10 000-100 000 000 yr. Inheritance, equifinality, and exhumation are commonly invoked to explain such landscape patterns, but are difficult to measure and thus test; here Africa's vast, deep regoliths epitomize the starkness of these challenges facing researchers across much of the continent. These deficiencies and problems are magnified when we consider the knowledge we seek of African landscape evolution toward resolving the complex history of the African plate since its individuation. The credentials of this knowledge are prescribed by the evidence needed to test competing hypotheses, especially invoking first order determinants of landscape dynamics e.g. membrane tectonics (Oxburgh ER & Turcotte DL 1974. Earth Planet. Sci. Lett. 22:133-140) versus plumes (Foulger G 2013. Plates vs Plumes: A Geological Controversy. Wiley Blackwell).

The evidence needed to test such competing hypotheses demands robust reconstructions of the individuated histories of landforms; in the African context, robustness pertains to the representativeness of events reconstructed in form and space (up to continental scales) and back through time from the Neogene into the Late Mesozoic. The ideal map of quantitative evidence must aim to integrate salient details in the trajectories of individuated landforms representing the principal landscapes of all Africa's margins, basins and watersheds. This in turn demands measurements - in mesoscale detail - of relief, drainage and regolith back though time, wherever keystone packages of evidence have survived Gondwana break up and its aftermath. Such a strategy is indeed ambitious, and it may well be dismissed as impractical. Nevertheless, the alternatives fall short. If it is to be representative of the history it purports to explain, we need the mesoscale facts to inform any narrative of a larger landscape (regional through to continental scales). Our ability to reconstruct narratives of landscape dynamics of encompassing – mega-geomorphic – patterns can only be as good as the details of individual events we can discern in Earth history.

Obviously, recognizing the centrality of "Conquering the Mesoscale" as the intrinsic prerequisite to test competing hypotheses of landscape dynamics, in the earth system context, calls for innovative research ap-

proaches. This is where Africa holds vast potential. The continent is the most remarkable natural laboratory to explore and tackle these challenges where we seek to build the composite mega-geomorphic chronicle informed in the detail of mesoscale process and form. But how does geomorphology, embedded in an earth system framework, advance beyond the established approaches in process and mega-geomorphology? The latter's limitations to reconstruct the tempo and mode of African landforms and palaeoenviroments reveal the stark limits for researchers. This is where a geobiological approach brings interesting opportunities, especially for Africa. Consider, for one, the interlinking patterns of high endemism and geographical heterogeneity of extant biodiversity across the continent, and moreover the interplay in biotic turnovers since the Mesozoic that shaped these regional and more local patterns. These individuated biotic assemblages making up the continent's biomes and ecoregions reveal strident congruence with physiographic controls: especially relief, drainage and edaphic variables. Calibrated by molecular clocks, resolved with DNA evidence, timetrees of this phylogenetic diversity reveal a richness of evolutionary signals; the spectrum of these spectacular biotic radiations of African biodiversity range from the Late Mesozoic to Recent. The temporal spread of this phylogenetic diversity is exemplified, for example, in the extant mammal fauna: witness the Afrotheria compared to the Bovidae (Kingdon J et al. 2013. Mammals of Africa. Bloomsbury Press). Equally, Africa's freshwater fish fauna stands apart in its high endemism, preponderance of highly specialized species flocks, and ancient lineages that have seeded recent radiations (Otero O 2010. Cybium 2010, 34(1): 93-113). Nevertheless, Africa's fossil record – botanical and zoological - is too patchy and incomplete to build palaeoenvironmental narratives with the precision needed to resolve details of mesoscale events in landscape dynamics (especially at timescales >10 000 yr).

Ideally, the biological evidence we seek to resolve a high fidelity narrative of landscape dynamics must extend back into the Cenozoic, and quantify turnovers of individual species on respective landforms. Births, deaths and tenures of species are its core currencies. The genomic record holds this evidence in its evolutionary archives, and we can read these signatures in the DNA of living organisms. This interdisciplinary approach exploits patterns of DNA variation in living organisms to reconstruct evolutionary events in landscape history at the mesoscale. Coupling the technological advances in 21st century molecular biology (especially genomics) with key tenets of ecological theory, we can exploit the remarkable variety of evolutionary signals preserved in the extant biodiversity of a landscape. Deciphering the genomic record, Geoecodynamics exploits the fidelity of individual species to their respective habitats; where the biota has persisted within/on encompassing landforms. This spatial resolution is determined principally by the degree of niche conservatism that has acted to lock the species into finite ecophysiological boundaries in the landscape. These ecophysiological envelopes of species can be mapped and modelled in a GIS framework, using variables familiar to geomorphologists: including altitude, surface roughness, lithology, and especially drainage attributes (stream topology and limnological variables). Geoecodynamics studies terrestrial and aquatic species as complementary biotic indicators of the palaeoenviroments in which they evolved. This strategy extends into the critical zone, to track evolutionary tenures and turnovers of endemics "ecological prisoners" in vadosic and phreatic landforms. Moreover, geoecodynamics of the Critical Zone can logically exploit endemic biota at the microscale in regolith, and also extremophiles to extreme depths; all such populations hold fascinating potential as biotic indicators of otherwise encrypted events in Earth history.

Geoecodynamics is an exciting area emerging in geobiology. It opens up with new lines of attack on challenges at the core of geomorphology and palaeoecology. In its abilities to quantify mesoscale phenomena, geoecodynamics injects new life into evolutionary geomorphology. Moreover, the means to quantify mesoscale process and form enables quantification of thresholds and tenures of landform dynamics; we can now scrutinize obscurities, including the scale-dependency of landscape events invoked to have shaped palimpsests (Brunsden D 1996 Zeitschrift für Geomorphologie NF, 40, 273– 288). Analogously, where accumulated packages of evidence survive, we should be able to map out key signals in the tempo and mode of the genomic record through the Critical Zone, and so scrutinize otherwise encrypted events that shaped the inherent emptiness of the Rock Record (Ager D 1993. The Nature of the Stratigraphical Record; Miall AD 2015. Strata and Time: Probing the Gaps in Our Understanding. Geological Society, London, Special Publications, 404, http://dx.doi.org/10.1144/SP404.4). Compared to, and notwithstanding, the episodic turnovers of sediments (and all allied events) that shaped evolving landscapes, the history of Life has been distinctly different; descent with modification links all clades and lineages of the Tree of Life with the present – even at deep nodes - though an unbroken chain of genomic connectivity. The complexity of niche space we see in landscapes reflects the diverse ways in how ecological fidelity of biodiversity maps on to landforms and their patchy environments, and this interplay has in turn acted to anchor evolutionary signals in the millions of individual species. The antiquity of African landscapes holds exciting opportunities for interdisciplinary explorations seeking mechanistic tests of this interplay between Process, Form and Life. The time is ripe to study African landforms and biota as a coevolving complex.

Key words: ontology, hierarchy theory, Individuality Thesis, Ghiselin, geobiology, geoecodynamics