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Biodiversity/Biodiversité

Biodiversity is not (and never has been) a bed of roses!

La biodiversité n'est pas (et n'a jamais été) un long fleuve tranquille !

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ABSTRACT

Over the last decades, the critical study of fossil diversity has led to significant advances in the knowledge of global macroevolutionary patterns of biodiversity. The deep-time history of life on Earth results from background originations and extinctions defining a steady-state, nonstationary equilibrium occasionally perturbed by biotic crises and "explosive" diversifications. More recently, a macroecological approach to the large-scale distribution of extant biodiversity offered new, stimulating perspectives on old theoretical questions and current practical problems in conservation biology. However, time and space are practically distinct, but functionally related dimensions of ecological systems. This calls for a spatially-integrated study of biodiversity dynamics at an evolutionary timescale. Indeed, the biosphere is a complex adaptive system whose study cannot be arbitrarily reduced to any single spatial- and/or temporal-scale level of resolution without a loss of content. From such an integrated perspective, a simple fact emerges: in a physically heterogeneous and ever-changing world, spatiotemporal variations in biodiversity are the rule–*not* the exception.

RÉSUMÉ

Ces dernières décennies, des progrès significatifs dans la connaissance des motifs macroévolutifs globaux de biodiversité ont été réalisés grâce à l'étude critique de la diversité fossile. L'histoire en temps profond de la biodiversité est un équilibre dynamique non-stationnaire d'apparitions et d'extinctions, occasionnellement perturbé par des crises biotiques et des diversifications « explosives ». Plus récemment, une approche macro-écologique de la distribution géographique à grande échelle des êtres vivants actuels a ouvert de nouvelles perspectives stimulantes sur de vieilles questions théoriques ainsi que des problèmes pratiques d'actualité en biologie de la conservation. Cependant, bien que distincts dans la pratique, temps et espace sont des dimensions fonctionnellement liées au sein des systèmes écologiques, plaidant de fait pour une étude spatialement intégrée de la dynamique de la biodiversité à l'échelle des temps évolutifs. La biosphère est un système adaptatif complexe dont l'étude ne peut être arbitrairement réduite à un seul niveau de résolution spatiale ou temporelle sans perte d'information. D'une telle perspective intégrée, un constat émerge : au sein d'un monde physiquement hétérogène et en perpétuel changement, les variations spatio-temporelles de biodiversité sont la règle et *non* l'exception.

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1. Introduction

Evolution enlightens all fields of biology through a single unifying principle: the descent with modification of individual organisms, making species varying through time, from generations to generations. As a consequence of the fine-tuning of genetic, developmental, physiological, and ecological processes enabling every organism to live in a given environment, conspecific individuals share common biological characteristics (inclusive of population polymorphism) that make up the functional identity and historical singularity of their community of reproduction. In spite of its still actively debated ontological and philosophical status, the biological species as a set of naturally and spontaneously interbreeding individuals that evolve in a unified way, thus appears as a fundamental unit of biological evolution and taxonomic classification [1,2].

From such an evolutionary perspective, biodiversity–the variety of life on Earth–can be viewed as the sum of all genetic, organismal and ecological variations (both compositional and functional) observed within and between species that coexist at a given time and place [3,4]. In this way, biodiversity goes far beyond the notions of taxonomic richness or abundance, as it also encapsulates genetic variability, morphological disparity, phylogenetic relatedness, trophic web structuring, etc. From genes to biomes and biogeographic kingdoms through individuals, (meta-) populations, species and ecosystems, such a multifaceted biodiversity is simultaneously the natural selection-driven cause and speciation-mediated consequence of evolution.

Whatever the natural group and environmental context under study, linking biodiversity with evolution makes worthy of attention two fundamental facts that emerge from the observation of ancient and extant life:

- continuously, new species originate, and others become extinct–the average duration of species as evidenced by the fossil record is 1–10 m.y. in order of magnitude, making the vast majority of genetic, organismal and ecological combinations that have existed on Earth already extinct–the few (tens of) millions of extant species are likely to represent ∼1‰ or less of all species that evolved on Earth;
- most of the identified fossil and living species show rather restricted geographic ranges corresponding to specific biogeographic and environmental conditions associated with the evolutionary history and ecophysiological characteristics (adaptations) of each species.

As a direct consequence, in a physically heterogeneous and ever-changing world, spatial and temporal fluctuations of biodiversity are the rule since the origin of life on Earth, thus legitimating two main questions:

- How does biodiversity vary through *time*?
- How does biodiversity vary through *space*?

Over the last several decades, these two questions have been addressed rather separately, the first one lying at the core of the Macroevolutionary research program [5–10], whereas the second one has more recently provided the basis for Macroecology, a research field concerned with the large-scale distribution and functional organization of life on Earth [11–15]. Nevertheless, while focusing on different topics (the analysis of global patterns and processes of speciation and extinction through time, and the descriptive and inferential spatial modeling of the ecogeographical distribution of biodiversity, respectively), these two questions are not independent: while in practice time and space are treated distinctly, they are functionally related dimensions of biological evolution (Fig. 1).

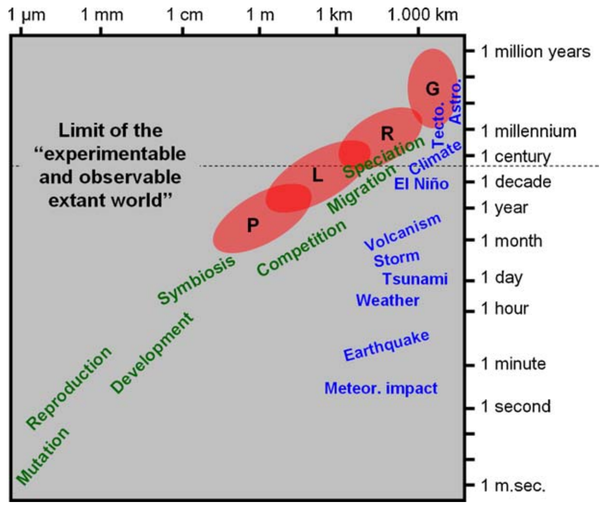

Fig. 1. Spatiotemporal scaling of selected physical/geological (in blue) and biological (in green) events (modified from [16]). The red ellipses roughly delimitate the four main spatiotemporal domains of descriptive biodiversity: P: point diversity; L: local community (α-) diversity; R: regional metacommunity (γ-)diversity; G: global diversity. The "limit of the 'experimentable and observable extant world'" is an empirical and pragmatic frontier in the scientific study of the Universe. Meteor. impact: meteoritic impact; Tecto.: plate tectonic activity; Astro.: astronomical cycles.

Such a spatiotemporal integration of biodiversity dynamics raises an operational difficulty: from the metapopulation and metacommunity regional level upward, the geographic and chronologic scales at which biodiversity changes (from hundreds to millions of square kilometers and years) are definitely inaccessible to experimental neontology. Instead, they require a deep-time historical perspective and hypothesis-testing approach based on the description and modeling of palaeobiological data coupled with *ex silico* simulation analyses [14,17–29]. Because the deep-time scale of species origination, evolution and extinction, is *de facto* the "maximum time scale" of the assembly, evolution and dismantling of local communities and regional metacommunities, a Macroecology not integrating the deep-time dimension offered by palaeontological data would be a myopic science condemned to never entirely and clearly see the object–definitely too large–of its study.

Hereafter we emphasize some aspects of this ongoing integration, highlighting already acquired results and suggesting future research opportunities.