

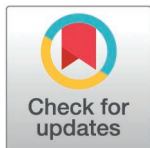
OPINION

Complexity and interpretability in global change ecology

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OPEN ACCESS

Citation: Montoya D, Burón-Ugarte A, Chrétien LTS, Christensen Garcia C, Granjel RR, Holmes M, et al. (2025) Complexity and interpretability in global change ecology. PLOS Clim 4(3): e0000587. <https://doi.org/10.1371/journal.pclm.0000587>

Editor: Jamie Males, PLOS Climate, UNITED KINGDOM OF GREAT BRITAIN AND NORTHERN IRELAND

Published: March 20, 2025

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Funding: This work was supported by the Spanish Ministry of Science & Innovation and by the European Social Fund through the Ramón y Cajal Program (RYC2020-028780-I), and the RECODYN Consolidator Grant funded by the European Research Council under the European Union's Horizon Europe (Grant Agreement Number 101043548).

Competing interests: The authors have declared that no competing interests exist.

Ecological systems are inherently complex. Global change- including the impacts of climate change- affects them in varied ways, and they respond in diverse forms. Any attempt to stem the current biodiversity crisis should account for this complexity while simultaneously reaching a general understanding of how ecological systems respond to global change. Here, we briefly introduce three axes of complexity in global change ecology and discuss how our approaches to understand it can be maximised.

The axes of complexity in global change ecology

Global change as a complex phenomenon

Global change encapsulates multiple factors (GCFs; [Fig 1A](#)). Land use changes result in the loss and fragmentation of natural habitats. Economies based on fossil fuels increase greenhouse gas emissions that impact the global climate, altering temperature and rainfall patterns. Pollutants are increasingly accumulated in natural systems in the form of pesticides, herbicides and (micro)plastics. Globalisation connects our world at unprecedented levels favouring the dispersion of species, making some of them invasive. GCFs vary in their frequency and intensity and are mechanistically different: habitat loss reduces species' carrying capacity; pollution reduces growth and/or increases mortality; invasive species affect species interactions. Further, GCFs act simultaneously and their interactive effects in ecosystems can be highly heterogeneous (synergistic—additive, multiplicative—or antagonistic) [[1](#)].

Ecological communities as complex systems

Ecological communities have multiple components (e.g., individuals, species), and are highly diverse both within species (intraspecific diversity) and across species (interspecific diversity). Species are embedded in complex networks of interaction types (e.g., mutualism, competition), non-randomly linked together and expensive to parameterise across environmental conditions ([Fig 1B](#)). Network approaches inform us both about who-eats-whom and on the importance of indirect effects among species. Therefore, species coexistence cannot be fully understood solely in terms of pairwise interactions but rather after accounting for the entire structure of the complex interaction networks that they form [[2](#)]. Ecological communities usually inhabit heterogeneous fragments connected by dispersal—metacommunities [[3](#)]—, are temporally dynamic, and change phenologically [[4](#)]. This biodiversity across space and time is responsible for the provision of essential ecosystem functions and services such as food

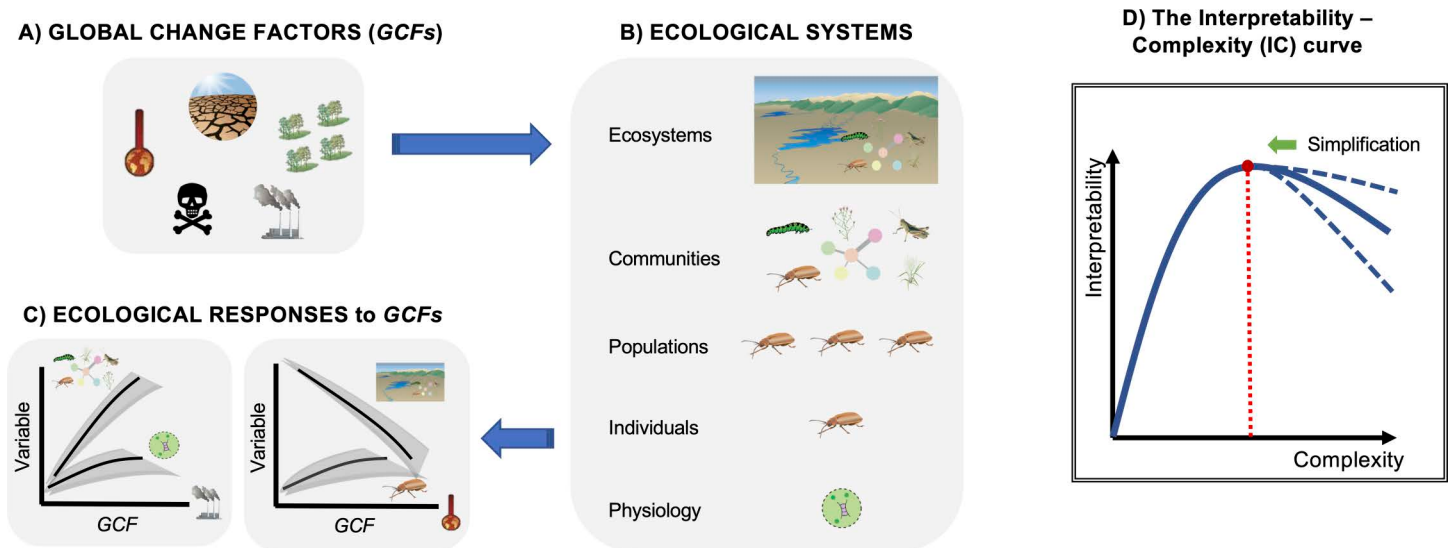


Fig 1. Complexity and interpretability in global change ecology. Three axes of complexity are represented: (A) Global change includes multiple factors (GCFs) that operate simultaneously and interact; (B) Ecological systems have multiple levels of organisation and display patterns at several spatial and temporal scales; (C) Ecological responses are often heterogeneous across GCFs and ecological scales. (D) The challenge in global change ecology is to try to find the maxima of the IC curve (red dot), i.e., the correct complexity (i.e., number of measured variables) to maximise interpretability.

<https://doi.org/10.1371/journal.pclm.0000587.g001>

provision, pest control, or climate regulation, as well as their stability (i.e., resistance, resilience, recovery, invariability) [5]. Ecological systems can be characterised by multiple facets which are not inherently related, i.e., changes in one variable do not affect other variables [6]; however, if related, such relationships are not necessarily proportional (e.g., existence of functional trade-offs [7]).

Ecological responses to global change

Ecological responses to GCFs are heterogeneous (Fig 1C). Species' sensitivity to habitat fragmentation depends on how connected the remaining fragments are perceived by species, which depends on their ability to disperse. Organisms' responses to changing temperatures are defined by their thermal performance curves, which are non-linear and vary across species. Differences in diet breadth determine species' resistance to GCFs: generalist consumers are more resistant to resource depletion and less prone to extinction. Community-level diet differences are captured by degree distributions, which often follow power-law patterns where most species are specialists. Because species respond to GCFs individually and often non-linearly (Fig 1C), a fundamental question arises: can we predict the response of multispecies communities to global change accurately if those responses are idiosyncratic?

Approaching ecological complexity: A journey towards interpretability

Simplifying complex systems is a necessary step to interpret them, or to have an idea of how uncertain we are about predictions to provide error margins for policy-making. Fortunately, although the phenomena and systems in global change ecology are complex, the way we measure them can range in complexity. The key question is: how much information is enough to understand ecological complexity? [8]

If we plot interpretability (defined as scientific understanding) as a function of complexity (defined as the amount of information to describe an ecological system—i.e., the number of measured variables—, not the “true” complexity of the system), this interpretability-complexity (IC) curve would be divided in two sections (Fig 1D). In the first section, at low information levels, the increase in the number of variables enhances our understanding or interpretability. This can be illustrated by research on diversity-function relationships. Initially, research was limited to measuring diversity as the number of species and considering single functions, typically plant biomass. The addition of more ecosystem functions, larger spatial scales and longer time-series increased the number and frequency of sampled variables, and also our understanding of diversity-function relationships. Therefore, we now know that diversity becomes more important for ecosystem functioning as we increase the number of functions and the spatial and temporal scales of analysis [9]. Additionally, whereas measuring single functions reduces sampling effort, understanding the ecological responses to global change is clearer when we know how multiple functions relate to each other (synergies, trade-offs [7]) and how such relationships are altered by global change. The same applies to the study of ecological stability and species interactions [10], where an increase in complexity is beneficial.

Does interpretability increase indefinitely with the number of measured variables? We contend that the IC curve is not linear for several reasons. First, a nearly inevitable property of measuring many variables is that of multicollinearity: many of them will be correlated and describe the same process. Secondly, too many variables increase the likelihood of including irrelevant information and of “fishing” for spurious statistical significance that hinders interpretability. This raises the question of which variables matter to understand the effects of global change on a given spatial, temporal, and ecological scale. Finally, a large number of variables may accurately fit natural phenomena, but constrain their mechanistic understanding (“black-box” scenario). Consequently, more information does not necessarily lead to higher understanding; rather, a higher understanding can actually be obtained by deleting unnecessary, redundant information. This underlies the second section of the IC curve: at very high information levels, interpretability is hampered. Using the diversity-function literature again, studies measuring a large number of ecosystem functions (e.g., the Biodiversity–Ecosystem Functioning Experiment China: <https://bef-china.com/index.html>) end up aggregating them into fewer dimensions describing a similar process, e.g., decomposition. Consequently, some simplification at high levels of information is required to better understand ecosystem multifunctionality.

Reducing complexity does not necessarily mean losing information; oftentimes, it means simplifying and/or rearranging existing information. We briefly describe common ways to reduce complexity below.

Aggregation

Aggregation groups variables using statistical methods (e.g., Principal Component Analysis, Non-Metric Multidimensional Scaling) or directly aggregating raw data. Examples include the aggregation of ecosystem functions (see above) but also functional classifications and response diversity. The former collapses species into groups according to their functional traits (e.g., the plant economics spectrum classifies traits along a slow-fast continuum [11]), the latter summarises the diversity of species responses to environmental change. Aggregations can improve our understanding of ecological systems: whereas functional classifications complement taxonomic information to better understand ecosystem functioning [12], response diversity has been identified as a crucial mechanism that synthesises community responses to environmental perturbations [13]. Finally, GCFs are also aggregated into categories that increase the predictability of their effects on ecosystems. Recent classifications are being proposed based

on the distribution of GCFs effects across targets (i.e., the ecological variables they affect most) and ecological scales (from physiological to community levels) [14].

Scale adaptation

Scale adaptation addresses the question of what information is relevant at which spatial, temporal, and organisational scale (cell vs. individual vs. population vs. community)? In physics, quantum theory nicely explains subatomic behaviours, and Newtonian mechanics accurately describe the movement of planets. Something similar applies to global change ecology: is there a spatial and temporal scale a particular GCF operates at (e.g., climate change vs. local pollution event)? What level of organisation does it affect most? Answering these questions narrows the scales of analysis and the variables of interest. Emerging classifications of GCFs' effects implicitly underscore the concept of scale adaptation [14].

Combination

Combination refers to the use of complementary methodologies, such as theoretical models and experimental manipulations [15]. To understand the individual and combined effect of multiple GCFs, experimental studies must adopt multifactorial designs that examine different GCFs combinations. Because each combination of 1-to-N GCFs must be replicated, multifactorial experiments with multiple treatments (and treatment levels) demand large replication numbers that are not always available. In these cases, models can simulate missed experimental treatments.

Conclusion

Whether we accept that reducing complexity is a flawed strategy or not, we often need to get rid of complexity to enable interpretability. The challenge in global change ecology is to try to find the maxima of the IC curve, i.e., the correct complexity to maximise interpretability and understanding.

Author contributions

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