Forum

Delayed biodiversity change: no time to waste

Franz Essl[1,2,3], Stefan Dullinger[3], Wolfgang Rabitsch[2], Philip E. Hulme[4], Petr Pyšek[5,6], John R.U. Wilson[1,7], and David M. Richardson[1]

[1] Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa
[2] Environment Agency Austria, Spittelauer Lände 5, 1090 Vienna, Austria
[3] Division of Conservation Biology, Vegetation and Landscape Ecology, Faculty Centre of Biodiversity, University of Vienna, Rennweg 14, 1030 Vienna, Austria
[4] The Bio-Protection Research Centre, Lincoln University, PO Box 84850, Canterbury, New Zealand
[5] Institute of Botany, Department of Invasion Ecology, The Czech Academy of Sciences, 252 43 Průhonice, Czech Republic
[6] Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, 128 44 Praha 2, Czech Republic
[7] South African National Biodiversity Institute, Kirstenbosch Research Centre, Claremont, 7735, South Africa

Delayed biodiversity responses to environmental forcing mean that rates of contemporary biodiversity changes are underestimated, yet these delays are rarely addressed in conservation policies. Here, we identify mechanisms that lead to such time lags, discuss shifting human perceptions, and propose how these phenomena should be addressed in biodiversity management and science.

Environmental change and delayed biodiversity responses

Biodiversity often does not respond immediately to changes in the physical or biotic environment. Considerable time lags (i.e., relaxation times) are involved in these responses [1,2]. However, the mechanisms at work, and the factors (e.g., feedbacks or abrupt changes at thresholds) that mediate delayed biodiversity responses to environmental forcing are manifold and poorly understood. Consequently, the full spectrum of consequences of rapid environmental changes on biodiversity is difficult to contextualize and, thus, the implications are easily underestimated. Here, we expand on recent assessments of these phenomena [2] by formulating 12 mechanisms that contribute to delayed biodiversity responses (Table 1), discuss how human perceptions regarding environmental change typically result in slow societal response, and then provide priorities for science and management on how to address this problem to mitigate future attrition of biodiversity.

Progress and limitations in understanding the mechanisms of delayed biodiversity responses

Delayed biodiversity responses to environmental forcing have been well studied over the past two decades, especially in the context of habitat loss and fragmentation. Mechanisms and implications have been intensively explored after the phenomenon of extinction debt was proposed by Tilman *et al.* [1], likely because habitat destruction is a dominant and clearly visible feature of environmental change and because it is relatively straightforward to quantify (e.g., by using time-series of changes in habitat extent that can be backcast using historical maps). However, recent work has highlighted that biodiversity shows substantially lagged responses to other changes in biotic and abiotic pressures (e.g., [3,4]), and more needs to be done to elucidate the consequences of these processes (Table 1). Moreover, studies on delayed biodiversity responses have usually focused on particular kinds of environmental change in isolation (e.g., habitat loss or range filling of invasive species) and on one or a few taxonomic groups. In reality, such changes often act simultaneously upon multiple components of biodiversity. For instance, habitat loss causes qualitative changes in the remaining habitat (e.g., due to edge effects), and alters connectivity between remaining habitat patches [4], simultaneously affecting genes, species, and communities. In the worst case, such changes result in losses of ecosystem services that contribute to human well-being, but often with delays of several decades [2,5].

Delayed biodiversity responses can, of course, lead to increases as well as declines in population sizes and species diversity in communities. Available evidence suggests that relaxation times arising from the same pressure differ in length for biodiversity losses and gains. For instance, projections of the ranges of plant species in mountains under climate change have suggested that range losses at the trailing edge will take longer to unfold than range gains at the leading edge [5], thus creating a transient species surplus.

Shifting baselines undermine the assessment of long-term environmental changes

Humans tend to undervalue environmental changes that unfold slowly and incrementally over timescales of decades relative to those that play out over a single human generation or less. In fact, assessments of environmental changes are often based on shifting baselines. As humans, we adjust our perception of the state of the environment unconsciously, based on recent impressions, giving scant attention to earlier changes [6]: the abnormal becomes the new normal. For instance, climate change during the 21st century will likely be drastic, and the global surface air temperature will probably exceed the limit of dangerous

Corresponding author: Essl, F. (franz.essl@univie.ac.at).
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Table 1. Twelve mechanisms that contribute to delayed biodiversity responses[a]

No	Mechanisms	Examples	Relevant species attributes	Consequences	Implications for management
1	Ecosystem loss (i.e., quantitative ecosystem change)	Forest clearing; conversion of grasslands to agricultural fields	Generation time; population dynamics; minimum viable population size	Delayed local population and/or species diversity decline and loss	Reserve planning and management; ecosystem conservation and restoration; long-term biodiversity monitoring
2	Ecosystem degradation (i.e., qualitative ecosystem change)	Input of nutrients; toxic substances; loss of ecosystem structures	Life-history traits that are relevant for the factor implicated in ecosystem degradation (e.g., sensitivity to toxic substances)	Delayed local population and/or species diversity decline and loss	Ecosystem management; long-term biodiversity monitoring
3	Changes to ecosystem connectivity	Increased fragmentation of ecosystem patches; increased connectivity (e.g., rivers connected by artificial waterways)	Dispersal capacity; (meta)population dynamics	Delayed increase in (meta)population extinction risk; delayed local population and/or species diversity decline and loss	Corridor planning; 'Green infrastructure'
4	Climate change	Range and abundance changes of species tracking climate change	Dispersal capacity; population dynamics	Delayed trailing and leading species range dynamics; delayed changes of species abundances	Monitoring of current and projections of future range and population dynamics; ecosystem-based adaptation
5	Changes in disturbance regime	Change in natural (e.g., fire, floods) and anthropogenic (e.g., traditional land-use) disturbance frequencies and intensities	Species ecology (e.g., serotinous species for changes in fire regime)	Delayed changes in species composition and ecosystem structures	Evaluate and integrate lagged biodiversity responses in the management of natural and anthropogenic disturbances
6	Changes in biotic interactions	Loss or establishment of biotic interactions (e.g., parasitic, symbiotic, or trophic)	Trophic position, species ecology	Delayed loss or establishment of biotic interactions; delayed reaction of indirectly affected species and/or trophic groups (e.g., pollinators as a consequence of a decline of plant species richness due to ecosystem loss)	Consider the indirect effects of lagged environmental change on biotic interactions in biodiversity management
7	Successional changes	Loss of late-successional ecosystem structures (e.g., old growth forest stands, or deadwood)	Association with late-successional stages	Delayed decline or loss of species restricted to late-successional ecosystem structures (e.g., deadwood)	Ecosystem management and conservation (e.g., reserve planning)
8	Changes in biophysical processes	Changes in cycles and stocks of matter and energy (e.g., biomass or nutrient cycling)	Species ecology	Delayed changes in cycles and stocks of matter and energy	Sustainable use of natural resources needs to take into account delayed responses of biophysical processes
9	Selective removal of species (overharvesting)	Fishing, hunting, poaching, and collecting wild plants	Interaction of the species with the removed species (e.g., prey or competition)	Delayed decline or loss of overharvested species; delayed indirect effects (e.g., mesopredator release); delayed genetic changes of the removed species (e.g., due to new size-specific selection pressure)	Accounting for population biology and demography and indirect effects when setting harvesting caps
10	Species transport or invasions	Anthropogenic translocation; introduction and spread of species	Association with human transport pathways; dispersal capacity; population dynamics	Delayed establishment, range filling and population density equilibrium	Preventive measures (e.g., regulations, border inspections, or phytosanitary measures); eradication and containment measures
11	Evolutionary changes	Evolutionary responses to environmental changes	Genetic diversity; adaptive capacity	Delayed evolutionary adaptation to changing forces	Monitor genetic diversity and consider programs to maintain diversity
12	Adaptive changes	Adaptive responses (e.g., behavior or phenology) of species to environmental changes	Phenotypic plasticity	Delayed adaptive changes to changing forces	Difficult to integrate into management decisions

[a]For further reading and references on these mechanisms, see for example, [2,4,12].

climate change of 2°C relative to 1850–1900 [7]. However, a temperature increase of 2°C corresponds to an average annual increase of only 0.02°C, and this warming trend is masked by substantial interannual to interdecadal climatic variability, thus making it barely discernible to humans. Such unconscious behavior undermines the full appreciation of long-term biodiversity changes and, thus, responses follow with concomitant time lags.

Implications for biodiversity research and management

Time lags caused by a range of mechanisms, which are often interacting, often are in the range of decades to centuries for ecosystems and ecosystem services [2,5]. Here, we identify 12 important mechanisms for delayed biodiversity responses, provide examples, and describe both their consequences and implications for management (Table 1). Given that these prolonged delays call for adjusting priorities for biodiversity research and management, we highlight five priority areas where action is most needed (Box 1).

Most importantly, the understanding of the scale of time lags must be improved and considered in biodiversity management (Priority 1). This can be achieved by expanding existing long-term ecological monitoring networks, such as GLORIA (http://www.gloria.ac.at) and ILTER (http://www.ilternet.edu), which concomitantly record changes in pressures and monitor pathways of biodiversity responses over long timescales, using shared protocols at a global scale. However, further initiatives designed to identify causal relations between pressures and responses are urgently needed for particularly vulnerable (eco)systems (e.g., coral reefs, wetlands, or Arctic environments). Another promising avenue for assessing and projecting long-term biodiversity lags is the integration of historical data on biodiversity pressures with contemporary data on biodiversity states and trends.

Recent reviews of trends in the global status of biodiversity indicate that, while some indicators of societal responses (e.g., extent of protected areas) have improved, most biodiversity indicators continue to decline [8]. To ensure that biodiversity indicators truly capture biodiversity trends, already known inertias in biodiversity responses (a factor not yet explicitly accounted for in these assessments) must be included to provide realistic biodiversity scenarios (Priority 2). Furthermore, interactions between mechanisms, as well as cascading effects, that cause cumulative time lags need to be taken into account (Priority 3).

For precautionary biodiversity management, the identification of robust early-warning signals (e.g., critical slowing down of recovery rates after perturbations) of approaching thresholds (tipping points) of losses of biodiversity or ecosystem services [9] is urgently needed (Priority 4). If biodiversity responses follow with substantial delay, such signals provide windows of opportunity for responses such as changes in reserve planning, land-use management, or fishery policies [9,10].

Finally, it is equally vital to counteract the detrimental implications of changing human perceptions (Priority 5). These can be achieved by defining benchmarks using remaining near-pristine reference systems or by reconstructing historic conditions against which to assess changes, and by using such reference states for setting catch quota or conservation targets (e.g., [11]), as done in the European Union Water Framework Directive (http://ec.europa.eu/environment/water/water-framework/index_en.html) for example. Equally needed are studies that disentangle the psychological mechanisms involved in shifting baselines of environmental assessment [6].

Box 1. Five priorities to inform policy to address delayed biodiversity responses

(1) Improve knowledge of the temporal dimension of time lags associated with different mechanisms involved in biodiversity responses and consider the outcomes of such lags in management decisions (e.g., reserve planning and management, ecosystem conservation and restoration, or spatial planning).
(2) Develop realistic long-term biodiversity projections by including inertias of biodiversity responses into biodiversity indicators and scenarios.
(3) Improve the understanding of interactions between mechanisms and of cascading effects of changing pressures through interaction networks within communities or ecosystems on resulting cumulative time lags of biodiversity responses.
(4) Improve the understanding of thresholds and tipping points, which can increase the magnitude of delayed biodiversity responses, and identify early warning-signals of approaching thresholds.
(5) Improve the understanding and make explicit the role of shifting baselines in assessing environmental changes.

Concluding remarks

The failure to give adequate consideration to the full range of mechanisms causing widespread time lags and shifting human perceptions masks the full extent of biodiversity changes that have already been triggered [2]. This situation calls for a strict application of the precautionary approach in biodiversity conservation and utilization (e.g., fishing quotas or Biodiversity targets for 2020, *cf*. https://www.cbd.int/sp/targets/) to ensure a safe operating space given that lagged biodiversity responses will never be fully accounted for. Furthermore, understanding and managing the inertia of biodiversity response requires a long-term biodiversity stewardship perspective [10].

The piecemeal understanding of delayed biodiversity changes driven by the multitude of increasing anthropogenic pressures has become a major barrier to an adequate response to the global biodiversity crisis. It is crucial that biodiversity initiatives such as IPBES (http://www.IPBES.net) and CBD (http://www.cbd.int) use their mandate to bring the likely consequences of delayed biodiversity responses to the forefront of the policy arena.

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