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Opinion Article

On the Need to Differentiate the Temporal Trajectories of Ecosystem Structure and Functions in Restoration Programs

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Abstract

Potential time lags between human-mediated disturbances and the subsequent responses of ecosystems are critical for planning and implementing conservation and restoration actions. In this context, decoupling between the temporal trajectories of ecosystems structure and functions is particularly critical. Here, we stand out the need to differentiate the temporal trajectories of ecosystem structure and functions to be considered in ecological restoration programs. In cases when ecosystem functions persist after the degradation of the ecosystem structure, and when functions do not recover at the same rate as structure, some kind of ecosystem functioning credits or debts can occur. In other situations, an ongoing loss of the ecosystem function can occur even in the absence of further disturbance. Ecosystem restoration outcomes could be optimized in regions with ecosystem functioning credit, since mitigating the decline in functioning will be more efficient than recovering functions in highly degraded conditions. Ecological restoration programs should not only focus on structure-derived indicators but they should also consider the dynamics of ecosystem functions to guide land-planning decision-making.

Keywords

degradation, disturbances, ecological restoration, ecosystem resilience, recovery debt

Structural diversity has been widely used in ecological restoration as a proxy to monitor the recovery disturbances in terrestrial ecosystems (Brancalion & Chazdon, 2017) and some crucial marine ecosystems such as coral reefs (Mumby et al., 2004). The rapid expanse of remote-sensing techniques now opens the perspective to use ecosystem structure measurements to monitor restoration success at large scales (Almeida et al., 2019; Mumby et al., 2004) such as when canopy cover—one of the metrics of forest structure—is associated with critical ecosystem services such as temperature regulation and water quality (De Frenne et al., 2019; de Sosa et al., 2018). However, ecosystem structure alone may not be a reliable proxy for biodiversity and ecosystem services. For instance, management can largely decouple structural diversity from species diversity in forest ecosystems (Brancalion & Chazdon, 2017).

Another major limitation of ecosystem structure for the monitoring of restoration projects is that habitat degradation can have temporally delayed adverse effects on biodiversity and ecosystem functions (Dullinger et al., 2013; Tilman et al., 1994). Following the disturbance, local extinctions of species may take years or decades, depending on their sensitivity to habitat modification (Brejão et al., 2018). This time lag between

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human-mediated disturbances and species extinctions is known as *species extinction debt* and has been a critical issue for conservation planning (Hanski, 2013; Tilman et al., 1994). Time lag responses to human-mediated disturbances have been explored under different ecological contexts but mainly focused on biodiversity conservation (Kuussaari et al., 2009; Rybicki & Hanski, 2013). This delayed species loss results in a decline of the ecosystem functions that these species support (Isbell et al., 2015). The "recovery debt" continues to affect ecosystems after the disturbance ceased, which not only impacts the biodiversity of restored areas but also functions such as carbon and nitrogen cycling (Moreno-Mateos et al., 2017).

The temporal trajectories of ecosystem functions are of crucial importance for conservation and ecological restoration planning (Ruiz-Jaen & Aide, 2005). Our current understanding of ecosystems indeed states that beyond a disturbance intensity threshold, the resilience of ecosystems decreases, and the resulting state of degradation may not be possible to revert, unless intense restoration efforts are applied (Melo et al., 2013; Suding & Hobbs, 2009). Conservation and restoration interventions should then be a prime concern in ecosystems that still are in a resilient state (Barlow et al., 2018; Hobbs et al., 2009). However, in degraded ecosystems, ecosystem functions may continue to decline as a delayed consequence of past disturbances, even if these disturbances ceased.

Additional to species loss, disturbances also affect ecosystem structure, which is an essential driver of ecosystem functioning and related service provisioning (Dubois et al., 2019; Gamfeldt et al., 2013; Gough et al., 2019). Similar to species persistence, ecosystem functions may not necessarily respond immediately to structural ecosystem degradation but might do so with a delay (Hamilton, 2011; Moreno-Mateos et al., 2012). In such a case, since a recovery debt is accumulating across time, urgent interventions are required to prevent further impacts on ecosystem services and human well-being. By contrast, the rapid recovery of ecosystem structure following a disturbance may not necessarily indicate a comparable recovery of ecosystem functions. It is likely that the influence of changes in structure—which include delayed effects—varies among ecosystem functions. Moreno-Mateos et al. (2017) reported that compared with reference levels, recovering ecosystems run annual deficits that are different for organism abundance (49%), for species diversity (31%), carbon cycling (38%), and nitrogen cycling (39%).

Here, we propose the need for a better embracement of the decoupling between the temporal trajectories of ecosystems structure and functions into ecological restoration programs. We describe a conceptual model of the links between ecosystem structure and functions across degradation and recovery processes and illustrate this model using examples drawn from the tropical forest and coral reef restoration.

Temporal Trajectories of Forest Structure and Functions

When ecosystem functions persist at higher provisioning levels than those expected by previous changes in the ecosystem structure, we consider that an ecosystem functioning credit is building. On the contrary, an ecosystem functioning debt would occur when ecosystem functions not recover at the same temporal rate as structure.

Different functions may follow particular response patterns to degradation and restoration, which have implications for restoration planning and payments for ecosystem service schemes (Figure 1). We assume that structure will never reach levels found in conserved, reference ecosystems, at least at a time scale relevant to present generations, and thus ecosystem functioning will not be fully recovered (Barlow et al., 2007; Gibson et al., 2011; Watson et al., 2018). More dramatic impacts are expected for functions performed by specific biological organisms, which may never be recovered if one or few species go extinct (Ellison et al., 2005).

In this model, a decrease in the ecosystem functioning following disturbance depends on structure loss and is specific to the resilience of each ecological function

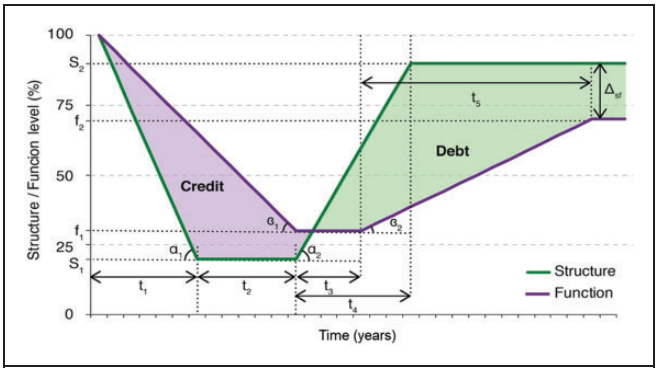


Figure 1. The Link Between Ecosystem Structure and Functions Across Degradation and Recovery Processes. During degradation, the ecosystem structure (green line) decreases until a level S_1 in t_1 years, with an α_1 angle of declination. The ecosystem function (blue line) may decrease by different dynamics, reaching level f_1 in $(t_1 + t_2)$ years, with a β_1 angle of declination. Structure declined faster than function, resulting in a credit of function (green polygon) by t_2 years time lag period. During recovery, the structure takes t_4 years to reach the maximum level (S_2) by a rate of increase represented by angle β_2. Following the declination curve, ecosystem function takes more time (t_5) to reach the maximum level (f_2), resulting in a debt of functioning. The difference between maximum levels of structure (S_2) and function (f_2) is represented by Δ_{sf}, while t_4 represents the resilience time between the starting points of the structure and functions recovery.

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(Figure 1). This decrease may be a decaying curve rate (β_1), time lag (t_3), and minimum level (f_1). Function improvement following structure recovery (parameters β_2, t_5, and f_2) is dependent not only on the same decaying curve but also on time lag (t_2) and ecosystem structure increment curve (parameters α_2, t_4). The area between structure and function curves along the degradation period quantifies the ecosystem function credit, while the area between these curves during the recovery period quantifies the ecosystem function debit. Considering the same period for ecosystem structure loss, stabilization and recovery (e.g., 30 years of forest degradation, followed by 30 years of agriculture), the ecosystem function credit derived from ecosystem degradation process may not be proportional to ecosystem function debit due to ecosystem recovery. The angles (α, β) between structure and function curves represent how directly linked are both and determine time lags that would affect credit and debit functions overtime. For example, wider angles mean higher time lags between changes in structure and functions and, on the other hand, tighter angles mean that both structure and function are intrinsically linked.

In the case of tropical forests, the dynamics related to changes in ecosystem structure and functions are substantial for several ecosystem services such as climate mitigation through carbon stocking and regulation of water supply. We exemplified our conceptual model by considering the case of a rapid and full deforestation of tropical forest, and its recovery after 30 years of agriculture. In this example, there may be a considerable time lag between forest structure loss and decay of functions as well as between structure and function recovery (Figure 2A). Changes in structure indeed happen within a few days and have delayed consequences on soil water permeability. Following the disturbance, the recovery of tropical forest biomass and structure is usually fast (Chazdon et al., 2016; Poorter et al., 2016), whereas the recovery of soil permeability lags behind forest structure (Zimmermann et al., 2010). A lesser intense forest structure disturbance such as selective logging also decreases the forest functions, but the recovery could be faster that after other stronger disturbances (Barlow et al., 2018). In this context, the same forest ecosystem undergoing various magnitudes of disturbance may exhibit varied resilience in functions (Johnstone et al., 2016), resulting in different credit and debit balances.

In the case of coral reefs, repeated disturbances, including cyclones, bleaching events, and crown-of-thorns sea star outbreaks, produce a drastic decline of living coral cover as well as a turnover in fish communities (Figure 2B). In addition, 10 years after disturbance, mobile herbivorous species increased in response to food availability, resulting in more biomass productions and more organized flow pathways, a decrease in flow diversity, loss of coral-dependent species, leading to evident changes at the structural and functioning levels (Pratchett et al., 2011). Even though species abundance and biomass recovered, the ecosystem structure lost complexity and lost 29% of its overall cycling efficiency through the food chain (Dubois et al., 2019). With a reduction in detritivorous species, the ecosystem is, therefore, switching from a productive state, mainly based on detrital pathways to a less productive state with slower nutrient cycling.

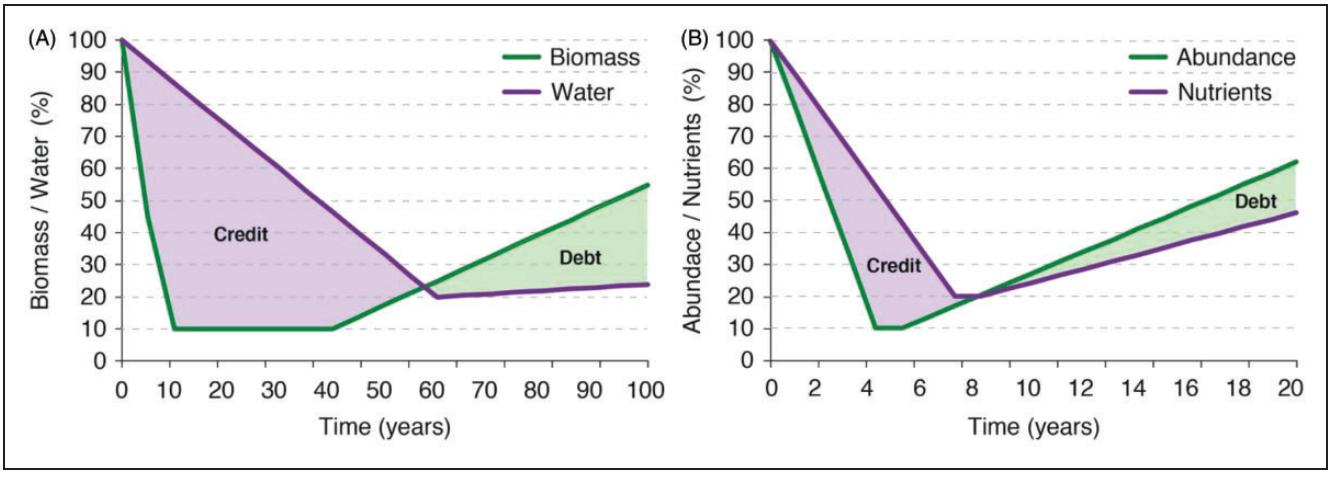


Figure 2. Panel A: Deforestation abruptly destroys forest structure but water infiltration in the soil maintains due to the high levels of organic matter that prevents an equally fast decline. After some years of intensive agriculture, however, infiltration continues to decline and stabilize at a suboptimal level. Aboveground biomass recovers fast through natural regeneration and reaches the predisturbance levels after a few decades (Poorter et al., 2016) but infiltration takes more time to reach desired levels. Panel B: Living coral cover declines by impacts of cyclones or sea star outbreak, resulting in less biomass and loss of ecosystem complexity and cycling efficiency. Species abundance and biomass recover after 10 years but cycling efficiency through the food chain does not (Dubois et al., 2019).

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Conservation and Management Implications

Considering the immediate and delayed responses of ecosystem functions to changes in ecosystem structures is critical for supporting decision-making programs focused on safeguarding or recovering ecosystem services at multiple spatial and temporal scales. This is particularly important considering individual disturbances, but specially interactions among disturbances and with climate change may combine to affect ecosystem resilience (Johnstone et al., 2016).

Our conceptual model can be applied beyond the two examples used in the previous section and described in a wide range of ecological contexts. For instance, in dry forests, hurricane disturbances appear to affect the forest structure on a long time scale rather than the functions, even though this effect is hardly distinguishable from the superimposed effects of other disturbances (Imbert & Portecop, 2008). In other cases, the recovery of total ecosystem carbon stocks after disturbance may produce an increase in the structural complexity of the forest canopy, which ultimately facilitates late-successional species recolonization, and thus effects may be most persistent for species composition (i.e., still significant 500 years after disturbance), while total carbon (i.e., a measure of ecosystem functioning) be less affected (effects scenarios until 236 years; Seidl et al., 2014).

Further studies are needed to understand the specific association patterns between ecosystem structure and functions, their time lags, and consequences for ecosystem services. Our proposed conceptual model should be adjusted to specific ecosystem structure and function based on field data to be applied: (a) in prioritization schemes such as payment for ecosystem services and restoration to optimize ecological return on investment (Hua et al., 2016; Rappaport et al., 2015) and ecosystem services (Ferraz et al., 2014); (b) to better inform policymakers and practitioners on the pros and cons of different strategies adopted in the emerging land degradation neutrality programs; (c) in the selection of management and restoration strategies that better match expected outcomes for ecosystem services provisioning; and (d) for improving existing ecosystem services monitoring and accountability guidelines, validating indicators of ecosystem structure that reflect changes in functions.

Hopefully, our proposal will foster a more pragmatic consideration of temporal dynamics of losses and gains in ecosystem functions in the context of ecosystem services programs, going beyond traditional targets that focus solely on the structure indicators and consider the link between structure and function as static. Ecosystems that appear resilient to disturbances can hide recovery debts, and the disturbance impact may propagate into other components or functions not directly exposed to the disturbance (Dubois et al., 2019). The use of tree or forest cover as a surrogate for estimating changes in biodiversity and ecosystem services has demonstrated being fallacious (Brancalion & Chazdon, 2017; Ferraz et al., 2014; Puyravaud et al., 2010), and new approaches are now needed to guide planning, implementation, and monitoring of environmental programs. Functionally based indicators, such as soil quality indices (Muñoz-Rojas, 2018), need to be tested and integrated into ecological restoration programs. Remote sensing has considerable potential for the large-scale monitoring of biodiversity and ecosystem functions that will benefit future restoration monitoring efforts (Asner et al., 2017; Schweiger et al., 2018). As humans rely on fully functioning ecosystems, recovery debt would expect to affect ecosystem services supply (Isbell et al., 2015) and be of pivotal importance for the sustainability of social–ecological systems (Lafuite et al., 2017).

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