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Ecosystem structure, function, and restoration success: Are they related?

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Summary

A direct relationship between ecosystem structure and function has been widely accepted by restoration ecologists. According to this paradigm, ecosystem degradation and aggradation represent parallel changes in structure and function, restoration following the same path as spontaneous succession. But the existence of single bidirectional trajectories and endpoints is not supported by empirical evidence. On the contrary, multiple meta-stable states, irreversible changes and hysteresis are common in nature. These situations are better described by state-and-transition models. Merging those models into the structure–function framework may help to develop new hypotheses on ecosystem dynamics, and may provide a suitable framework for planning restoration activities. We use the relationship between ecosystem function and the effort needed to restore a degraded ecosystem (i.e. restorability) as an example. A linear relationship between ecosystem structure and function suggests that ecosystem degradation and restorability are directly related. This may not be true when multiple states, not necessarily connected, are considered. We show two case studies that support this point, and discuss the implications of the incorporation of state-and-transition models into the structure–-function framework on relevant topics of restoration ecology and conservation biology, such as the choice of reference ecosystems, the evaluation of restoration actions, and the identification of priority areas for conservation and restoration.

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Introduction

The fast rate at which natural ecosystems are destroyed by human activities, and the increasingly reduced area occupied by intact ecosystems worthy of protection, has emphasised the importance of ecological restoration to maintain the Earth's natural capital (Young 2000). Due to the widespread extent of degraded ecosystems, and to limited funds typically available for natural resource management, selection of the areas and ecosystem components to be restored is one of the major challenges facing scientists and practitioners world-wide. Despite being crucial, it is difficult to conduct a practical assessment of whether a particular landscape is in need of restoration, and if so, which ecosystem components or functions should be restored first. This task can be optimised if the functional status of ecosystems can be defined beforehand, if the relationship between ecosystem structure and functioning can be established, and if the potential for ecosystem restoration is known.

Given its importance and implications for ecosystem management and restoration, it is not surprising that a large number of conceptual models have been developed by restoration ecologists to describe how ecosystem structure/composition and functioning are related (e.g. Bradshaw 1984; Francis, Magnuson, Regier, & Talhelm 1979; Hobbs & Norton 1996; Lockwood & Samuels 2004; Zedler & Callaway 1999). Among them, the model proposed by A.D. Bradshaw for the reclamation of derelict land (Bradshaw 1984; hereafter Linear Structure vs. Function model or LSF) has been one of the most influential and widely used by restoration ecologists and practitioners. This model assumes a parallel change in structure and function in aggrading and degrading ecosystems, i.e., a linear increase in ecosystem function with the increase in the complexity of its structure (Fig. 1).

In the context of the LSF model, structure can be any description of community composition, and the way organisms are organised (species and complexity, in the original formulation by Bradshaw 1984), and function encompasses surrogates of ecosystem functioning (standing biomass, nutrient accumulation). According to this model, restoration is defined as the simultaneous increase in structure and function promoted by human intervention, and it parallels changes occurring during secondary succession.

The LSF model has a strong heuristic value, it has been extremely successful in capturing the essence of ecological restoration, and it has inspired many restoration practitioners and casual users. However, as it is commonly used, it fails to reflect many real situations, and it may lead to excessively narrow definitions of reference ecosystems, and to erroneous estimations of the effort needed to restore degraded ecosystems. Here we review some of the assumptions of the LSF model on the basis

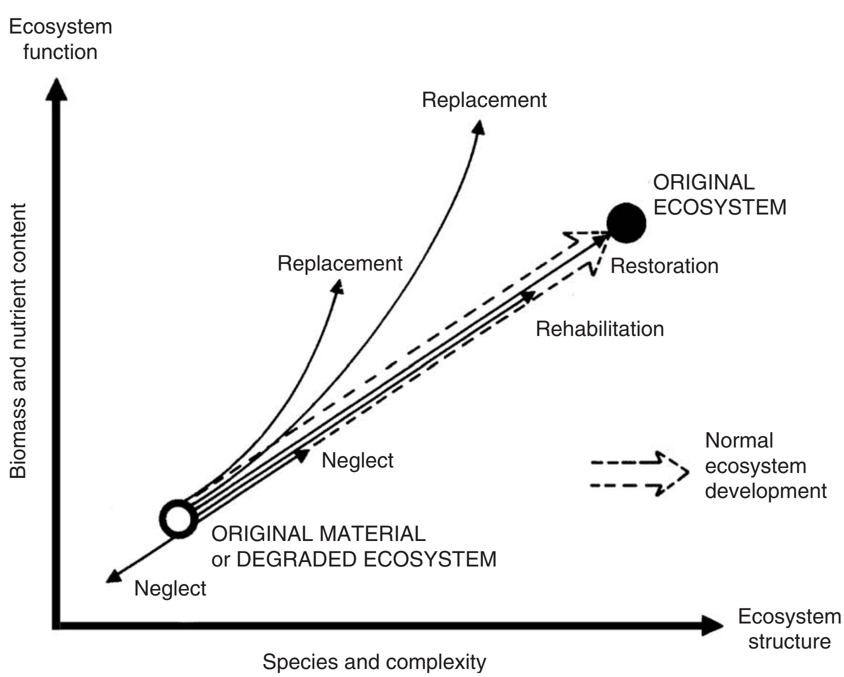

Figure 1. Graphic representation of the structure–function model. Reproduced with permission from Bradshaw (1984).

of current ecological knowledge, and discuss its capacity to predict ecosystem restorability (sensu Lindig-Cisneros, Desmond, Boyer, & Zedler 2003). We finally suggest an alternative model, based on state-and-transition models, that incorporates multiple meta-stable states, irreversible transitions and hysteretical dynamics.

On the assumptions of the structure–function model

Ecosystem structure and function may not change harmonically

A key assumption of the LSF model is the linear and positive relationship between ecosystem structure and function. Studies evaluating the relationship between community composition and ecosystem functioning have shown that a straightforward universal relationship between both sets of ecosystem attributes is not evident, particularly under field conditions (Hooper et al. 2005; Huston et al. 2000). For example, negative relationships between biodiversity and productivity have been frequently reported in the literature (Bakker & Berendse 1999; Drury & Nisbet 1973). Successional trajectories also show a high degree of variability in the rates and direction of changes in ecosystem structure and function (Debussche, Escarre, Lepart, Houssard, & Lavorel 1996; Tilman 1987).

Direct and indirect competition among organisms, and the effects of ecosystem engineers, may preclude the existence of positive structure–functioning relationships (Lepart & Escarré 1983; Wright & Jones 2004). On the other hand, arrival of a new species does not always translate into measurable changes in ecosystem function. Very often, species differ in their impact on ecosystem function by orders of magnitude (Hulbert 1997), and the effect of a particular species on ecosystem function may be low. Similarly, species loss is not always accompanied by functional decline, or at least not at the same rate (Ostfeld & LoGiudice 2003; Smith & Knapp 2003).

Degraded and reference ecosystem states are two of a range of alternative ecosystem states

Implicit in the LSF model is the notion of a linear trajectory and a single final ecosystem state, following Clementsian successional trajectories. It is interesting to note that Clements postulates were much richer than the often simplified climax-driven linear succession (Allred & Clements 1949). A.D. Bradshaw also warned about the existence of alternative states (Bradshaw 2002). Alternative meta-stable states in the structure–function space have been frequently reported in the literature (Anand & Desrochers 2004; Beisner, Haydon, & Cuddington 2003; Scheffer, Carpenter, Foley, Folke, & Walker 2001), and have been the basis for state and transition models (Hobbs & Norton 1996; Miles 1984; Yates & Hobbs 1997). These models, however, have been typically based on ecosystem structure, with a few exceptions (Falk 2006; Whisenant 1999). A major consequence of the LSF model is that degradative and aggradative trajectories follow the same track in the structure–function space. However, changes in structure and function in degrading ecosystems may not be identical as changes occuring when the pressure is released, hysteresis being common in community and landscape dynamics (Beisner et al. 2003; Higgins, Mastrandrea, & Schneider 2002). Hence, shifts between two different structure–function states may not necessarily follow the same trajectory.

Degradation and restoration thresholds

Restoration is commonly considered as accelerated succession (Hilderbrand, Watts, & Randle 2005). Changes in ecosystem structure and function may not be gradual, but show sudden changes. Degradation thresholds affecting ecosystem structure and function have been widely described in the literature (Scheffer et al. 2001; Whisenant 1999). In contrast, restoration thresholds, that is the occurrence of abrupt changes in ecosystem structure and function in response to a given restoration effort, have received less attention (Lindig-Cisneros et al. 2003; Suding, Gross, & Houseman 2004). The use of disturbances such as fire for ecosystem restoration is a good example of the relevance of restoration thresholds (Falk 2006). Such changes may result in low probability of occurrence of particular combinations of ecosystem structure and function between areas of higher probability.

The structure–function model revisited

We believe that only by active debate and questioning of paradigms such as the LSF model, can a full understanding of the influence of ecosystem's attributes on their functioning and restorability be achieved. We suggest that the LSF model should be expanded to integrate non-linear, even negative, relationships between ecosystem structure and function, and alternative ecosystem states (Fig. 2), in a similar way as state-and-transition models do on the basis of community composition. These modifications are based on current ecological knowledge on biodiversity–function relationships and succession theory, and have profound implications on many theoretical and applied aspects of ecological restoration and conservation biology that have not been fully explored so far.

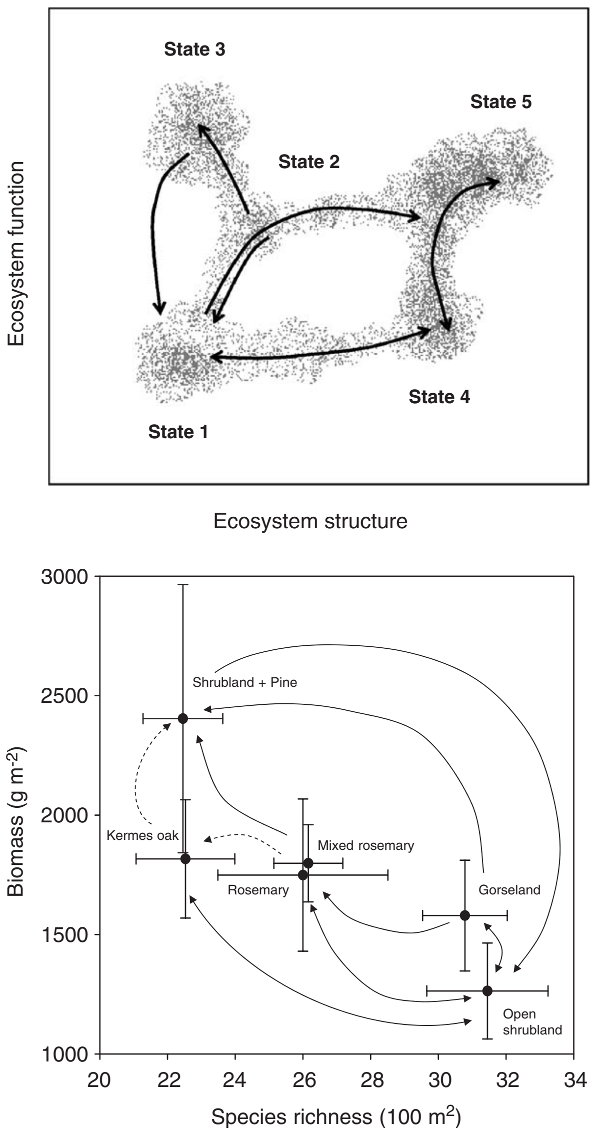

Figure 2. A conceptual model of ecosystem dynamics based on changes in ecosystem structure and function (top), and its application to a Mediterranean landscape of E Spain (bottom; adapted from Baeza, Valdecantos, Alloza, & Vallejo submitted). Meta-stable states (point clouds), hystheresis (contrasted upward and downward transitions between States 1 and 3), and thresholds (direct arrow showing no intermediate states in the transition from State 3 to 1) are illustrated in the conceptual model. States were identified by multivariate floristic analysis in the Mediterranean landscape example. Arrows show transitions between alternative states. Broken lines indicate transitions of low probability. Note that some arrows are bi-directional. Data represent means ± standard deviations of $n = 10-26$ plots. Kermes oak: *Quercus coccifera*, rosemary: *Rosmarinus officinalis*, gorse: *Ulex parviflorus*, Pine: *Pinus halepensis*.

State-and-transition models recognise that multiple successional trajectories are possible, and that alternative meta-stable states can exist under the same environmental conditions (Hobbs & Norton 1996; Yates & Hobbs 1997). Different states represent areas of higher probability in the structure–function space, and may result from gradual or sudden changes in ecosystem attributes. When defined in terms of ecosystem structure and function, alternative states can be targeted as reference ecosystems for restoration, provided that a particular combination of both sets of variables suits society interests (Hobbs & Norton 1996). Such models can also define transitions that are feasible and those that are not (e.g. direct transitions between State 3 and State 5 in Fig. 2), and may help to identify restoration techniques needed to bring the ecosystem to a desired state. In this wider context, restoration encompasses independent changes in structure and function, and multiple alternative states may not constitute partial steps towards restoration (Hilderbrand et al. 2005; Yates & Hobbs 1997), but alternative potential reference states.

The existence of irreversible transitions and hysteretical dynamics has major consequences for ecological restoration. On the one hand, when aggradative and degradative trajectories differ, restoration may need to use by-passes to reach a particular reference ecosystem, and thus additional efforts (particularly in terms of research and adaptive management) may be required. The good news are that restoration may not need to follow the entire sequence of degradation stages to reach the target ecosystem, but may 'jump' over partially degraded ones. For example, a narrow interpretation of Clementsian theories of succession has dominated much of the afforestation programmes in the Mediterranean Basin during the last century. In this area, conifers are particularly resistant to the stressful conditions of degraded ecosystems, are considered pioneer species, and have been extensively planted in countries such as Spain, Turkey, Italy, Algeria and Morocco (Pausas et al. 2004). One of the arguments used for the widespread utilisation of *Pinus* sp. in restoration projects is its role as a pioneer species. It has been largely assumed that *Pinus* sp. favour the establishment of late-successional hardwood species by improving soil conditions and ameliorating harsh microclimatic conditions under its protective canopy (Montero & Alcanda 1993). Late-successional hardwoods are demanding species, at least at the seedling stage (Cortina et al. 2004), and have been frequently considered unable to establish in open areas (Montoya 1988). However, recent data show that 'late-successional' hardwood species may be able to establish in degraded areas with no conifer facilitation (Caravaca et al. 2003; Jiménez, Navarro, Ripoll, Bocio, & De Simón 2005). And indeed, under semi-arid conditions, conifers may preclude the establishment of keystone hardwood species (Maestre, Cortina, Bautista, & Bellot, 2003; Maestre, Cortina, & Bautista 2004).

Another consequence of the incorporation of state-and-transition models into the structure–function framework is that the effort needed to restore a degraded ecosystem, may not be directly related to its integrity (as defined in terms of ecosystem structure and function), as the LSF model suggests. Provided that different alternative states in the structure–function continuum are possible, but all transitions between these states may be not, we can envisage a situation where restoration of a target ecosystem may be more easily achieved from a highly degraded state (in terms of structure, function or both), than from a relatively intact one (e.g. from States 2 and 3 to State 5 in Fig. 2). This is in agreement with the lack of consistency in the species richness–invasibility relationship (Chapin et al. 2000; Prieur-Richard, Lavorel, Linhart, & Dos Santos 2002), and has significant implications on the identification of priority areas for conservation and restoration. Below we present two case studies where a positive relationship between ecosystem functional status and restorability is not evident.

Ecosystem function and restoration in semi-arid steppes

In the Western Mediterranean Basin, semi-arid areas are frequently dominated by open steppes of the tussock grass *Stipa tenacissima* L. (alpha grass). Alpha grass steppes are impoverished in vascular plants. Sprouting shrubs, which were once part of the community, such as *Rhamnus lycioides* L., *Pistacia lentiscus* L., *Quercus coccifera* L., and *Juniperus oxycedrus* L., do not show evidences of active recolonisation, despite the presence of isolated extant individuals. Remnants of these shrubs play key functional and structural roles in semi-arid *S. tenacissima* steppes (Maestre 2004; Maestre & Cortina 2004, 2005).

We have used a degradation gradient of *S. tenacissima* steppes to evaluate the relationship between restorability (i.e. the difficulty in bringing a degraded ecosystem to a desired target state, or the effort needed to do so; Lindig-Cisneros et al. 1999), and degradation state. We selected a total of 17 sites within a 60 $\times$ 40 km area around Alacant (SE Spain), which showed contrasting signs of degradation but had limited variation in elevation, slope angle, orientation, lithology, and soil type (see Maestre 2004; Maestre & Cortina 2004 for details on site selection and characteristics). We measured restorability as the probability of survival of planted *Pistacia lentiscus* L. seedlings, a keystone species in alpha grass steppes (Maestre & Cortina 2005) which is commonly used in restoration programmes (Cortina et al. 2004).

To our surprise, we found that survival was lower in the steppes located at the highest altitudes and with the highest values of total plant cover, species richness, shrub cover and functionality (Fig. 3; Maestre, Cortina, & Vallejo 2006). Despite the evident shortcomings of an observational study, our results show that there may be exceptions to the direct relationship between ecosystem degradation and a relevant step in the restoration process, and suggest that further research on this topic is needed.

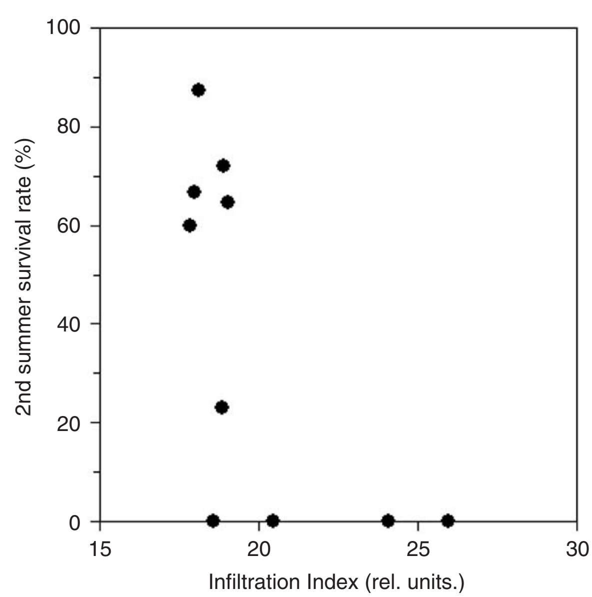

Figure 3. Second year survival of *Pistacia lentiscus* seedlings planted on a gradient of degraded *Stipa tenacissima* steppes. Landscape function (Infiltration index) was estimated according to Tongway and Hindley (1995). Original data from Maestre et al. (2006).

Forward and backward shifts in *Quercus suber* L. forest restoration

Under Mediterranean conditions, highly disturbed forest landscapes are often dominated by shrublands. In many cases, shrublands show relatively high levels of soil protection, resilience, and other functional ecosystem attributes (Vallejo, Aronson, Pausas, & Cortina 2006), and may constitute a cultural value in themselves. Still, reversion to forest may be desirable for various reasons, including cultural appreciation for forests and trees (Ginsberg 2006).

We recently evaluated the effect of shrubland management on the establishment of *Quercus suber* (cork oak) in Serra Espadà (E Spain). Forests dominated by this species cover more than 2.5×10^6 hectares in the Western Mediterranean basin, and have great ecological, economic and cultural values (Montoya 1988; Vieira Natividade 1991). However, they have been substantially reduced in the past due to allocation to other land uses such as agriculture and grazing (Parsons 1962).

We compared the establishment of *Q. suber* seedlings within the shrubland and in cleared areas, and found that the negative effects of shrub species—probably resource competition—outbalance positive ones, such as climatic improvements because of shade (Fig. 4). In addition, spontaneous seedling establishment is low in unaltered shrublands, even in the vicinity of acorn bearing *Q. suber* trees (Pons & Pausas, submitted for publication). Thus, a critical step in *Q. suber* forest restoration, such as the establishment of the species itself, is more likely under conditions of lower ecosystem functionality. A net negative effect of the interaction between shrubs and planted *Quercus* sp. has been observed elsewhere (albeit not always; Johnson, Shifley, & Rogers 2002), and they may reflect cases of arrested succession or culs-de-sac in successional trajectories. Under these conditions, a disturbance such as clearing may be necessary to bring the ecosystem to a desired state.

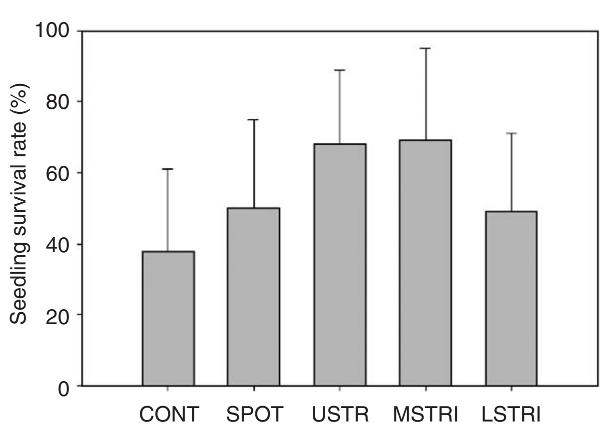

Figure 4. Effect of shrubland management on survival rates of *Quercus suber* seedlings one year after planting. CONT: undisturbed shrubland, SPOT: 2 m diameter clearings, USTRI, MSTRI and LSTRI: upper, middle and lower parts of a 5 m wide cleared strip. Bars correspond to means $\pm$ standard errors ($n = 3$ replicated plots).

Concluding remarks

State and transition models have been successfully used to describe ecosystem dynamics (Herrick, Bestelmeyer, Archer, Tugel, Brown, 2006; Herrick, Schuman, Rango 2006; Miles 1984), and to explain steps towards reference ecosystems (Hobbs & Norton 1996; Lockwood & Samuels 2004; Yates & Hobbs, 1997). We suggest that state and transition models should be incorporated into the structure–function framework. This may result in different combinations of structure and function of higher probability, linked by intermediate states defining trajectories in this space, as shown in Fig. 2.

Merging state-and-transition models into the structure–function framework allows for more plasticity in selecting target (reference) ecosystems, that can be defined in terms of desired ranges in composition and function. Multiple targets have been often recognised in ecological restoration, but they are usually associated with incomplete recovery and restoration failures (Aronson, Floret, Le Floc'h, Ovalle, & Pontanier 1993; Hilderbrand et al. 2005). Target ecosystems may be selected among non-functional but diverse ecosystems, or be justified by the presence of a species of particular interest. Society may choose among the multiple possibilities offered by this framework (including a third vector to integrate ecosystem goods and services; Aronson, Clewell, Blignaut, & Milton 2006; Cairns, 1993; Ginsberg 2006). This formulation of state and transition models allows quantitative definitions of relevant concepts in ecological restoration such as degradation, rehabilitation and reclamation.

According to the proposed approach, evaluation of restoration success should focus not only on reference ecosystem traits, and the degree of ecosystem integrity achieved by restoration actions, but also on current ecosystem state and ecosystem dynamics. This has multiple implications at the management level. For example, evaluation of restoration success should take into account the departing point as well as the likelihood of attaining a target state (Hobbs & Harris 2001). This is particularly relevant, considering that the effort needed to restore a given ecosystem (i.e. ecosystem restorability) may not always be directly related to current ecosystem functional status, as suggested by the examples described above. The model proposed here, integrates restoration and conservation actions based on changes in the disturbance regime, species removal, manipulations of ecosystem function, and species introduction, into a common framework. This array of situations can not be explained by the LSF model.

We identify three major challenges for restoration ecologists in this area: (1) to characterise potential ecosystem states in terms of ecosystem structure and function, (2) to identify transitions between states and determine their viability, and, particularly, (3) to evaluate the effort and eco-technological means needed to achieve the desired changes, and maintain the ecosystem in a given state. These are challenging tasks because of the intrinsic difficulty in restoring complete ecosystem attributes (Lockwood & Pimm 1999; Walker & Del Moral 2003; Young, Petersen, & Clary 2005), and because variables defining ecosystem structure and function may respond in different ways (Lindig-Cisneros et al. 2003; Zedler & Callaway 1999). However, the potential rewards in terms of optimisation of restoration actions are equally large (Herrick, Bestelmeyer et al., 2006; Herrick, Schuman et al., 2006). Further research is needed to advance in the incorporation of state-and-transition models into the structure–function conceptual framework, and to promote the implementation of this approach by land managers and restoration practitioners.

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