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Viewpoint

The dark side of the “redundancy hypothesis” and ecosystem assessment

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ABSTRACT

Intricacy of biotic interactions (predator-prey relationship, strength of food web links and other type of intra- and inter-specific relationships), as well as shifts in species functions in ecosystems, could affect the accuracy of predictions derived from the theory of redundancy of species, when applied to ecosystems assessment.

This opinion paper is based on three main considerations: 1) some fundamental differences between ecological and engineering definition of “redundancy”, underlying the main concerns related to the use frameworks derived from economical or engineering disciplines, as the ecosystems services paradigm; 2) presence of empirical obstacles to establish whether two different species are fully or partially redundant. When species redundancy in a particular community is estimated using a matrix with species-specific functional traits, often forgetting potential biotic interactions not directly related to the trophic chains or neglecting the variability in strengths of the links connecting these species; and 3) recent evidence offered by studies that shed doubts on the validity of the ecological redundancy hypothesis.

Finally, we claim that more attention must to be paid to intrinsic ecological aspects of ecosystem components (*per se* values rather than derived values), and a precautionary principle is necessary for decisions related to the assessment of ecosystems.

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1. Ecological complexity: not only a question of numbers

In this note, we underline some issues related to the use (and abuse) of a framework derived from disciplines such as economics or engineering, in ecological studies. We highlight how the complexity of biotic interactions could make the predictions derived from the theory of redundancy less effective (Walker, 1992), when applied to ecosystem assessment. We claim that more attention must to be paid to the intrinsic ecological aspects of ecosystem components (*per se* values rather than derived values).

The study of ecosystems is an important applied discipline suitable for understanding global change and human impact on environments (Raudsepp-Hearne et al., 2010). For this reason,

predominant directions in the study of ecosystems include a growing focus on human-dominated landscapes and the development of the concept of ecosystem services for human resource supply and well-being (Carpenter et al., 2009). Key ecosystem processes include primary production, evapotranspiration, respiration, decomposition, secondary production, soil formation and cation exchange, nutrient mineralization and immobilization, and many others (Currie, 2011). Nowadays, a major challenge is to ensure the functioning of ecosystem services to meet the needs of a burgeoning world population of humans (Biggs et al., 2012; Millennium Ecosystem Assessment, 2005). Ecosystem services are by definition the “benefits that people obtain from ecosystems” (Millennium Ecosystem Assessment, 2005). However, even if ecosystem services are a successful concept, they need much deeper theoretical development (Currie, 2011; Morelli and Møller, 2015). One good example of the need for potentially better understanding of the concept of ecosystem services is when this concept is linked to the redundancy hypothesis, originally related

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to the concept of ecosystem stability, but currently extended also to ecosystem assessment. The definition of “ecological redundancy” is based on the functional traits of species present in a given community. But this approach has proven to provide an incomplete framework for ecosystem assessments due to the complexity of ecological systems.

Even if a variety of definitions of complexity exists, the ecological complexity is mainly associated with two aspects: complicatedness (defined as the quantity of components), and hierarchical complexity (the levels of arrangement in the components) (Kolasa, 2005; Ricard, 2003; Van de Vijver et al., 2003). This statement means that the ecological complexity is not a simple count of components or relations among them, but also a question about the strength of bonds among components (Kolasa, 2005). The main type of biotic interactions constrains the spatial distribution of species/individuals across several mechanisms, such as predation, competition, resource-consumer interactions, host-parasite interactions, mutualism and facilitation (Bascompte, 2009; van Dam, 2009; Wisz et al., 2013b). We define the complexity of biotic interactions among species, populations or individuals as the intricacy of biotic relationships at different levels: from the complexity of the food web to the variability in each single biotic interaction: i.e. the non-linearity of predator-prey dependencies and their temporal fluctuation, vast array of feeding interactions, interaction of horizontal and vertical diversity (Duffy et al., 2007), antagonistic and mutualistic networks, as well as other biotic interactions unrelated to food chains and cascades of interactions (Allesina and Tang, 2012; Askeyev et al., 2010; Bondavalli and Bodini, 2014; Eklöf et al., 2013; Jochner et al., 2016).

For Bak et al. (1988) the species in an ecosystem support each other in several ways, which cannot be understood by studying the individual constituents in isolation: a point of view strongly linked to complexity theory. Complexity theory emphasizes self-organization of the components of an ecosystem, and supports the idea that there is no central control or master plan (Currie, 2011). Organism assemblages fulfill a critical set of ecological functions for ecosystems (Barbet-Massin and Jetz, 2015). However, each particular species plays a different role in the ecosystem; a role that could be more or less unique (or redundant) (Naeem, 1998). Increasingly, the role of biodiversity on ecosystems requires a clear understanding of the roles of species richness and species composition in communities (Downing and Leibold, 2002). It has been demonstrated that diversity in traits among species and derived functional diversity controls ecosystem functioning more

often than does species number (Mulder et al., 2012; Scherer-Lorenzen, 2005).

2. Diversity and ecosystems stability: persistence, resistance and resilience

The relationship between diversity and stability of ecosystems has fascinated ecologists for many years (Borrelli et al., 2015; McCann, 2000; Namba, 2015; Schleuning et al., 2015). The diversity-stability-hypothesis has a long history from its initial proposition (Elton, 1958; MacArthur, 1955; Odum, 1953), with a temporary disappearance of consensus (May, 1973), to more recent evidence suggesting that diversity begets stability (Kinzig et al., 2002; McCann, 2000). Currently, more evidence supports the hypothesis that the stability increases following the number of links in a food web, while restricted diet reduces stability. If the number of prey for each species remains constant, more species in the community will increase stability (MacArthur, 1955). However, nowadays the debate over the relationship between complexity of ecosystems and ecological stability is far from settled. Some recent papers, in fact, did indicate how the question is hard and how the relationships between stability and ‘complexity’ could be positive, neutral, or even inverse (Allesina and Tang, 2015, 2012; Altena et al., 2016; Namba, 2015).

Following Scherer-Lorenzen (2005), ecosystem stability is divided into three aspects: (i) persistence: the tendency to exist in the same state through time; (ii) resistance: capability to remain unchanged in the face of external pressures or disturbances; and (iii) resilience: ability to return to its original or equilibrium state after it has been displaced from it by external pressures. The term “resilience” was introduced to the field of ecology in the 1970’s by Holling (1973) as “a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables”. Resilience is often defined as “the ability of a system to absorb disturbances and still retain its basic function and structure” (Walker and Salt, 2006) and “the capacity to change in order to maintain the same identity” (Folke et al., 2010) (Fig. 1B). However, stability can also be defined as the size of perturbation needed to cause a change in identity of the system, while resilience can be associated to the ‘elasticity’ of the system: the rate of change of an output divided by the rate of change of an input during perturbation. Under these statements, ecosystems can be classified into 4 groups: brittle (high resilience, low stability); flexible (low

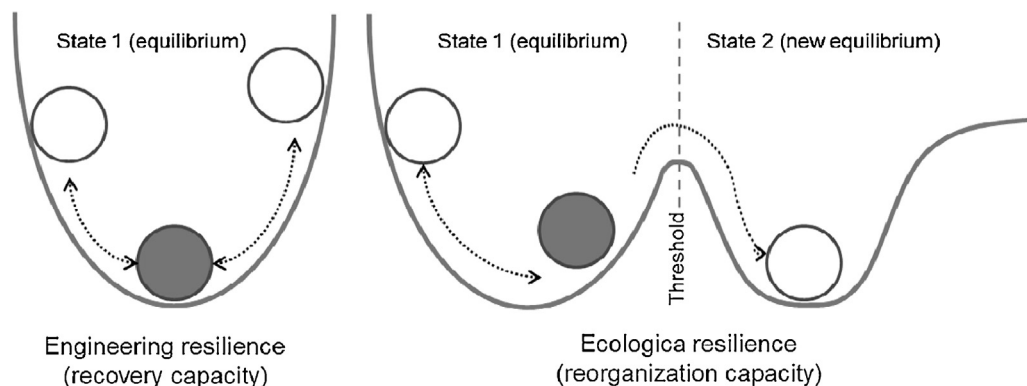


Fig. 1. The concept of engineering (A) and ecological (B) resilience illustrated by the simplification with the ball-and-cup heuristic. The cup represents the region in the state space, in which the system tends to remain, and includes all possible values of system variables of interest. The basin represents the different regimes that the system can assume without loss of identity (source: Liao, 2012).

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