Ecological Indicators 66 (2016) 76–85

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Assessing the persistence capacity of communities facing natural disturbances on the basis of species response traits

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ARTICLE INFO

Article history:
Received 24 July 2015
Received in revised form 8 January 2016
Accepted 13 January 2016

Keywords:
Response diversity
Redundancy
Disturbances
Resilience
Resistance

ABSTRACT

Adequately assessing the ecosystem resilience and resistance is a challenging and essential question in the current context of widespread environmental change. Here we suggest the use of a quantitative measure we call Persistence Index (PI) to assess the capacity of communities to maintain their functions and services after disturbances. First, we present the formulation of PI that is based on the diversity, abundance, and redundancy of disturbance- and taxon-specific response traits. Then, we use simulated data sets to study the effects of species richness and the number and frequency of traits on PI values. Finally, we illustrate our approach by assessing the persistence capacity of forest communities in Peninsular Spain and the Balearic Islands in response to fire, drought and windstorm events.

The Persistence Index was found to be relatively independent on the number of considered traits, but variable according to the frequency of traits in the community. In the evaluation made with national forest inventory data, PI was found to vary within and among different forest types, being particularly high in stands dominated by non-native species (e.g. *Eucalyptus* sp.) or in mixed-stands composed by evergreen and deciduous broadleaf species. We also found PI values to increase with the number of species present in the stand, although this relationship saturated due to overlap in species response traits.

The presented index is complementary to other approaches developed to study the functional structure of communities through the distribution of species in a functional space. It can be applied to a broad spectrum of communities subjected to different types of stressors, making it a useful tool to guide ecosystem management decisions in a context of changing climate and uncertain disturbance regimes.

1. Introduction

The management of natural resources has historically assumed environmental factors to remain relatively constant in time (Puettmann et al., 2013). However, this assumption is often no longer valid due to the increasing variability and uncertainty of driving forces, primarily climate (Lindner et al., 2010; Turner, 2010). Expected future changes in climatic conditions and socio-economic contexts lead to focus management efforts on preserving the ecosystems persistence and associated services (Allen et al., 2011; Folke et al., 2004; Gunderson, 2000; Oliver et al., 2015; Rist and Moen, 2013). According to Carpenter et al. (2001), assessing the persistence of ecosystems in the long-term requires to consider resilience and resistance as complementary concepts. Resilience is generally defined as the ability of ecosystems to undergo disturbance without shifting to an alternative state and losing its functions and controls (Gunderson, 2000), whereas resistance relates to the amount of external pressure needed to bring about a given amount of disturbance (Carpenter et al., 2001). Both concepts are considered essential to maintaining ecosystem functions, and they have been extensively developed (Brand and Jax, 2007; Lake, 2013). However, translating these concepts into practical operational indicators poses a major challenge since they are not easy to quantify (Lake, 2013; Rist and Moen, 2013).

The persistence of ecosystem properties and services can be approached through the assessment of the value, range and relative abundance of the species functional traits in a given ecosystem, understanding as functional traits those features of species considered relevant to their response to the environment (response traits) and/or their effects on the ecosystem functioning (effect

Abbreviations: PI, Persistence Index; RTR, Response Trait Richness; RTA, Response Trait Abundance.

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http://dx.doi.org/10.1016/j.ecolind.2016.01.024
1470-160X/

traits) (see Diaz and Cabido, 2001; Díaz et al., 2007). This trait-based approach is gaining currency for resilience assessments of different ecosystems (Chillo et al., 2011; Kahiluoto et al., 2014; Laliberté et al., 2010; Oliver et al., 2015; Puettmann, 2011; Standish et al., 2014), and it ties into the insurance hypothesis, which posits that the greater the diversity of responses among species providing a given function, the lower the risk this function will be dramatically affected by changing events (Yachi and Loreau, 1999).

Up to now, several indices based on the range of species traits have been proposed to measure the components of functional diversity (FD) (i.e. functional richness, functional evenness, and functional divergence, *sensu* Mason et al., 2005). These indices aim at quantifying complementary characteristics of the distribution of species and their abundances in a multidimensional space whose axes represent functional traits (i.e. functional space *sensu* Mouillot et al., 2013). The more different the species in a community are, according to their traits, the higher FD values are and the higher the probability that a given ecosystem function is maintained. Accordingly, some FD indices have been suggested as good indicators to assess changes in community assembly processes along stress gradients (Mason et al., 2013; Mouchet et al., 2010; Mouillot et al., 2013).

In general, most of the FD approaches measure the range and diversity of trait values among the different species in a community (i.e. they appraise the presence of species with contrasted trait values). However, very few approaches have been developed based on the presence and abundance of specific traits that confer species with the ability to cope with changes (hereafter response traits). Some recent works have nevertheless proposed the use of response-and-effect frameworks in which relevant traits to the resistance and recovery of species are grouped according to functional groups (Neill and Puettmann, 2013; Puettmann, 2011) or related to the environmental variability (Sterk et al., 2013). Despite being promising methods to understand and assess ecosystem persistence to environmental variability and disturbances, neither provides a quantitative measure of the presence of certain trait values that are key to the ecosystem persistence.

Here we present a new index that can be used to assess the capacity of communities to maintain their functions when subjected to a given set of disturbances. We consider that ecosystem functions and services are potentially persistent when the species involved in their provision present traits that confer them resilience and/or resistance to their main stressors.

In the following, we first explain the rationale and calculation of the proposed Persistence Index (PI). We then use Monte Carlo simulations to illustrate its behavior under different conditions of trait frequencies and availability of trait information. To better understand the relationship between the PI and other indices, we compare PI values with other indices of taxonomic and functional diversity. Finally, to evaluate the performance of the index with real data, we apply our approach to tree communities across all forests in Peninsular Spain and the Balearic Islands. In particular, we assess how the PI is affected by species richness (i.e. the number of species) and how it varies within and across forest types. In the discussion, we show the main strengths and pitfalls of PI and discuss potential applications of the method.

2. The Persistence Index

2.1. Rationale of the index

The Persistence Index (PI) attempts to quantify the adaptive capacity of communities to disturbances. The index is based on the general assumption that an ecosystem will be more resilient and resistant to disturbances if it contains a greater presence of species with a given set of response traits (Elmqvist et al., 2003; Puettmann, 2011). PI integrates three different components related to the ecosystem persistence capacity: (i) the number of response traits present (Chillo et al., 2011; Elmqvist et al., 2003; Mori et al., 2013a; Newbery and Lingenfelder, 2009); (ii) the abundance of species presenting response traits, assuming that the more abundant these species are, the more likely the functions they provide to the ecosystem will persist after a disturbance; and (iii) the redundancy of response traits across species, which insures ecosystems against decline in their functioning thanks to the overlap in species response strategies (Yachi and Loreau, 1999).

2.2. Requirements and formulation

The design of PI is simple and flexible enough to be applicable to many kinds of communities, regardless of the set of species considered and the disturbances affecting them. To calculate PI in a particular target community, the required inputs are: (1) the set of species that are relevant for the persistence of the desired community state and/or function; (2) the main disturbances threatening the community's state and/or function; (3) the response traits that confer species with the ability to resist or recover from these disturbances; and (4) the abundance of species in the community. The method requires a species-specific response trait matrix $\mathbf{V} = \{v_{i,t}\}$, of dimensions $S \times M$, where the values of S species for M traits are stored. Values in $\mathbf{V}$ must be either quantitative or binary, although quantitative data need to be standardized to the [0,1] interval prior to computing the index. It is also possible to use qualitative data if previously transformed into dummy binary variables, but missing values are not allowed (see Section 3.2 for an example of imputation). The index allows weighting response traits using a vector $\mathbf{w} = \{w_t\}$ (where w_t is the weight assigned to response trait t) for cases where not all response traits are considered equally relevant with respect to the set of disturbances under study. Finally, the method also requires, for each target community, a vector $\mathbf{x} = \{x_i\}$ containing the relative abundance of the $i = 1, \ldots, S$ species. Species relative abundances are bounded between 0 and 1. They may be defined relative to the total abundance in the community (and hence be considered proportions and the sum is one) or relative to an arbitrarily fixed maximum abundance value (e.g. see definition of $\mathbf{x}$ in Section 3.2). For the process of selecting the response traits, taxonomic levels other than species can be considered, but it is important to select traits with low variability within the considered taxon so as to avoid assigning incorrect trait values. For example, if we are considering species as the target taxonomic level, we should avoid response traits with high intraspecific variability.

PI is formulated as the product of two components, which we call *response trait richness* (RTR) and *response trait abundance* (RTA), and that are considered equally relevant to the persistence capacity of communities:

$$\mathrm{PI} = \mathrm{RTR} \cdot \mathrm{RTA} \tag{1}$$

The product of the components allows obtaining high values of PI just when both RTR and RTA are relatively high, and penalizes its value when either RTR or RTA is low.

The response trait richness (RTR) component measures *the proportion of response traits present in the target community* with respect to the total number of traits selected as relevant to cope with the considered disturbances, and is calculated as:

$$\mathrm{RTR} = \frac{\sum_{t=1}^{M} w_t \cdot \max(v_{1,t}, \ldots, v_{S,t})}{\sum_{t=1}^{M} w_t} \tag{2}$$

where w_t is the weight assigned to response trait t and $v_{i,t}$ is the value of response trait t for species i.