



Biomass-dispersal trade-off and the functional meaning of species diversity



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ABSTRACT

Production–diversity patterns lack a single explanation fully integrated in theoretical ecology. An ecological state equation has recently been found for ruderal vegetation. We studied 1649 plots from twenty-nine ecological assemblages and analyzed the relationship between diversity, biomass and dispersal looking for a pattern across these ecosystems. We found that high biomass and low dispersal values were significantly associated with high diversity plots under stationary conditions, and vice versa, involving a biomass-dispersal trade-off that is coherent with well-established ecological principles. Therefore, energy per plot, estimated as one half of the product of mean individual biomass and mean square dispersal multiplied by the number of individuals per plot, only reaches its maximum at intermediate levels of diversity. This explains the well-known humped relationship between production and diversity. We also explore why the rest of the diversity–production patterns can be explained starting from disruptions of this basic pattern. Simultaneously, the product of diversity, biomass and square dispersal is statistically equal to the ecological equivalent of the Boltzmann's constant included in the ecological state equation that remains valid for all the assemblages explored due to scale variations in the value of the above-mentioned constant. Biomass-dispersal trade-off resembles the principle of equipartition of energy from the kinetic theory of gases but in a characteristic way, because the alternative micro-associations of dispersal-biomass in function of species diversity are not randomly distributed as it happens with the combinations of molecular mass and velocity in a mixture of gases. Therefore, this distinctive ecological feature should be assumed as one of the main pro-functional gradients or thermodynamic constraints to avoid chaos and ecological degradation under stationary conditions. Hence, biomass-dispersal trade-off explains production–diversity patterns and the ecological state equation in simultaneous agreement with conventional ecology and physics.

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1. Introduction

The relationship between species diversity and ecosystem functioning is one of the most important points for ecosystems

conservation (Tilman, 1999; Hector et al., 2001; Willig, 2011). For instance, diversity and trophic production can be associated according to the following patterns: (a) a unimodal hump-backed curve (e.g. Chase and Ryberg, 2004; Graham and Duda, 2011); (b) direct linear (e.g. Marquard et al., 2009; Li et al., 2012); (c) inverse linear (e.g. Moser and Hansen, 2009); there may also be (d) no evidence of any significant relationship (Huston et al., 2000; Long and Shaw, 2010), or even more than one of these patterns can emerge

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for a single taxocene depending on the observation scale (Zhang and Wang, 2012). The proportions of these four patterns according to a survey of the ecological literature including a total of 200 cases (Waide et al., 1999) are 30%, 26%, 12% and 32%, respectively.

Such a variety of patterns may be due to: (i) the absence of simple laws at the biological community level (Lawton, 1999; Simberloff, 2004); (ii) the spurious influence of variables not explicitly included in the analysis (Mouquet et al., 2002; Hawkins et al., 2003; Mittelbach et al., 2003); or (iii) methodological issues (Huston, 1997; Naeem and Wright, 2003; Gamfeldt and Hillebrand, 2008).

Alternatives (ii) and (iii) may share a common cause due to the use of surrogate indicators instead of direct measurements. For example, the number of species (richness) is frequently assumed to be a good indicator of diversity, on the one hand, and biomass a good measure of production on the other. However, this procedure to evaluate production–diversity patterns has been questioned (Whittaker and Heegaard, 2003; Dangles and Malmqvist, 2004; Wilsey et al., 2005).

According to the conventional concept of biological diversity (Magurran, 2004, p. 17), the assumption that richness can replace diversity leaves evenness (i.e. the relative abundance between species) out of the analysis. Similarly, the assumption that biomass can replace production neglects the fact that production is the flow of energy that sustains standing biomass (Odum, 1968, 1969).

On the other hand, an ecological state equation (ESE, Eq. (7), below), similar to the ideal gas state equation, has recently been found for ruderal vegetation (Rodríguez et al., 2012). In comparison with the well-consolidated theory regarding the thermodynamic nature of the ecosystem (Odum, 1968, 1969), the ESE is, for the moment, an empirical result restricted to a particular kind of ecological assemblage. Thus, three main issues should be clarified: Can it be assumed that the ESE is a general pattern under stationary conditions (SC)? What is the ecological foundation of this equation? Is there any reliable reason to consider this equation as unconnected from the conventional ecological theory?

In this article, we develop an all-encompassing explanation of the above-mentioned issues that becomes a general exploration of the functional meaning of species diversity including several new findings. With such a goal, we examine the relationship between diversity and a proxy for trophic production calculated in a similar way to that of kinetic energy in physics. As a result, we found a biomass–dispersal trade-off (B-DT) that explains production–diversity patterns in agreement with conventional ecology and physics. We also obtained a general validation of the ESE for all the stationary systems sampled, confirming at the same time the congruence of this equation with well-established ecological principles. Finally, we discuss the general meaning of these findings.

2. Materials and methods

2.1. Indicators

(a) Species diversity per plot (Shannon, 1948; Magurran, 2004):

$$H_p = - \sum_{i=1}^S \frac{n_i}{N_p} \ln \frac{n_i}{N_p} \quad (1)$$

where S is the species number per plot; n_i is the number of individuals or colony elements (e.g. corallites) of species i ; N_p is the total number of individuals per plot = $\sum n_i$.

(b) Total biomass per plot (m_{eTp}) and mean individual biomass per plot (m_e) in kg: biomass has been recognized as one the most

important indicators to describe ecological dynamics at any hierarchical level (e.g. Margalef, 1963; Odum, 1969; Bombelli et al., 2009).

(c) Ergodic (transitivity or meaning equivalence between space and time from the analytical point of view, see Appendix A, pp. 1–3) indicator of dispersal activity (Rodríguez et al., 2012):

$$I_e = \frac{\sum_{i=1}^S (I_{ei,j})}{S} \quad (2)$$

$$I_{ei,j} = \left(\frac{d_{i,j}}{s_{i,j}} \right) \times 100 \quad (3)$$

$$d_{i,j} = \frac{\sum_{k=1}^m ((\sqrt{(x_j - x_k)^2 + (y_j - y_k)^2}) \times (2i_{j,k}/i_j + i_k))}{m} \quad (4)$$

where $d_{i,j}$ is the mean dispersal activity of species i in plot j with central geographic coordinates (x, y) within a total space s_0 divided into an m number of k plots; i_j and i_k are the respective abundances of i in plots j and k ; $i_{j,k}$ is the shared number of individuals of i in plots j and k (e.g. if $i_j = 7$ and $i_k = 12$, then $i_{j,k} = 7$); $(2i_{j,k}/(i_j + i_k))$ is the Bray-Curtis similarity index (Washington, 1984); $s_{i,j}$ is the standard deviation of $d_{i,j}$ (given that $d_{i,j}$ is an arithmetic mean); $I_{ei,j}$ is the ergodic indicator of dispersal activity of species i in plot j ; I_e is the ergodic indicator of dispersal activity of the species group in plot j ; and S is the species number in plot j . $\sqrt{((x_j - x_k)^2 + (y_j - y_k)^2)}$ is the Pythagorean theorem that allows the estimation (see Eq. (4)) of a mean Euclidean distance between plot j and all the remaining k elements within the set of m plots. The calculation of I_e regarding 3D space (coordinates x, y, z per plot) only requires the replacement of $\sqrt{((x_j - x_k)^2 + (y_j - y_k)^2)}$ by $\sqrt{((x_j - x_k)^2 + (y_j - y_k)^2 + (z_j - z_k)^2)}$. The calculation of I_e , heuristically explained in seven steps, is as follow: (Step 1) Can we consider the distance reached by a species i starting from an arbitrary x, y or x, y, z point within a stationary system as a good indicator of dispersal capability? Yes \Rightarrow Euclidian distance calculation (EDC; the left element on the numerator of Eq. (4)). (Step 2) EDC, assumed as a single vector-parameter for dispersal, has a drawback: its modular value for all the valid cases ($i_j \neq 0$ and $i_k \neq 0$) is the same either if $i_j = i_k$ or if $i_j \neq i_k$. Nevertheless, it is obvious that, for instance, when $i_j = 100$ and $i_k = 1$ our certainty about the real dispersal capability of species i would be considerably lesser than when $i_j = 100$ and $i_k = 100$. This limitation should be solved \Rightarrow see step (3). (Step 3) The Bray-Curtis Similarity Index (BCSI) can function in this case in a similar way to a relative probability (since it is ranged from 0 to 1 with 1 value only if $i_j/i_k = i_k/i_j = 1$) that either maintains or discounts a given amount from the modular value of EDC depending on the degree of quantitative similarity between i_j and i_k : if $(2i_{j,k}/(i_j + i_k)) = 1$ the result from $EDC \times BCSI = EDC$, but it is proportionally shorter as $(2i_{j,k}/(i_j + i_k)) < 1$. Therefore, the value of BCSI can be used as a probabilistic assessment of our certainty regarding EDC \Rightarrow calculation of $EDC \times BCSI$ (numerator of Eq. (4)) as a whole. (Step 4) The mean value of $EDC \times BCSI$ for species i in plot j in regard to all the remaining k plots included in the total set of m plots will indicate the mean dispersal capability of i taking j as a reference point $\Rightarrow d_{i,j}$ calculation (Eq. (4)). (Step 5) However, two equal means can be obtained from two very different set of data \Rightarrow see step (6). (Step 6) What species would have a higher dispersal capability according to the distribution of its $d_{i,j}$ values? That species (generally, a dominant species) whose distribution of $d_{i,j}$ values is as homogeneous as possible regarding all the set of m plots. The coefficient of variation ($CV = s/\mu \times 100$; where s :

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