

Neutral Theory of Biodiversity and Prediction in Ecology¹

Teoria Neutrale della Biodiversità e Previsioni in Ecologia

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Riassunto: Una delle principali sfide dell'ecologia moderna è quella di fornire la base conoscitiva per prevedere variazioni della biodiversità in relazione ai cambiamenti delle condizioni ambientali. Le capacità predittive delle teorie ecologiche sono tuttavia limitate dalla enorme variabilità che caratterizza i sistemi naturali e dalla loro complessità. La Teoria Neutrale della Biodiversità assume che le specie sono equivalenti su base pro-capite nella risposta ad eventi di disturbo e nelle capacità ad acquisire risorse. Basandosi unicamente su processi demografici fondamentali quali natalità, mortalità e migrazione di individui, la teoria ha mostrato capacità predittive considerevoli in vari sistemi terrestri ed acquatici. Questo studio combina analisi correlative ed esperimenti di campo per esaminare in quali circostanze oltre a generare previsioni corrette, la teoria identifica correttamente i meccanismi che ne sono alla base per cui l'assunzione di equivalenza risulta giustificata.

Keywords: Biodiversity, Environmental variance, Neutral Theory, Prediction, Species Abundance Distributions.

1. Introduction

Predicting changes in numbers, identities and abundances of species in space and time is a fundamental goal of ecology. The precision and accuracy of ecological predictions is often limited by the large variability inherent to ecological systems. The Neutral Theory of Biodiversity (NTB) explains biodiversity changes on the basis of fundamental processes of birth, mortality and migration of individuals (Hubbell 2001). This theory has the potential to predict various ecological patterns, including species-areas relationships, island-mainland dynamics and species turnover in space and time. A fundamental assumption of the theory is that species within a given trophic level are equivalent on a per-capita basis – i.e. there are no species-specific traits that differentiate the response of species to environmental processes. According to the theory, changes in assemblages occur as a consequence of random processes of

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mortality induced by natural or anthropogenic disturbance and subsequent colonization of the vacant space.

The only mechanism invoked by the theory is dispersal limitation. This implies that the new individuals colonizing after disturbance may originate in part from nearby populations, in part as migrants from distant populations. Thus, local assemblages of species are connected through dispersal and are in fact organised in meta-communities. Changes in abundance of species in space and time result from random events of mortality and colonization leading to what has been termed ecological drift. This is analogous to the neutral drift described in genetics (Kimura 1983).

The NTB is a sampling theory – i.e. it is described by parameters that can be estimated from samples providing the basis for testing the theory (Alonso et al. 2006). There are two fundamental parameters: θ , the fundamental biodiversity parameter, which reflects the regional pool of species or regional diversity, and m , the migration parameter reflecting the fraction of new individuals migrating from other populations during colonization. These parameters can be estimated by fitting the so called Zero-Sum Multinomial Distribution (ZSM) to species abundance data. Indeed, there are two versions of the theory, one specified only by the parameter θ , which does not include dispersal limitation and applies to the meta-community (mZSM distribution) and another that includes dispersal limitation and therefore parameter m , which applies to local communities (lZSM). Analytical solutions have been provided to fit the two distributions to empirical data using maximum-likelihood estimation.

The NTB has been tested by comparing the fit of the lZSM and mZSM distributions with that of alternative theories of species abundance distributions like Fisher logseries (Fisher et al. 1943) and Preston lognormal (Preston 1948). Most tests have used data from terrestrial vegetation although examples of studies conducted in aquatic systems exist. Two general lines of consensus have emerged from these analyses. First, the logseries and lognormal distributions are now recognized as special cases of the NTB, corresponding to the mZSM and lZSM distributions, respectively. Second, and more importantly, neutral dynamics and non-neutral processes (i.e. those that ascribe ecological differences to species and include density-dependent processes) are not mutually exclusive views of assemblage structure and dynamics. Thus, the relevant research issue is to determine in which environmental conditions and at which spatial and temporal scales the NTB provided a sufficient model to describe and predict assemblage dynamics. To address this issue, correlative analyses based on observational data need to be integrated by experimental tests of hypotheses about the response of assemblages to environmental change.

In this study, I use data on assemblages of algae and invertebrates of rocky shores to test predictions of the NTB. First, I examine whether temporal patterns of decay in assemblage dissimilarity observed over a period of 15 years are consistent with the patterns predicted by the NTB under ecological drift. Second, I use data from an experiment on disturbance and recovery to test the prediction that changes in temporal variance of disturbance alone – i.e. with no concomitant changes in intensity – would not affect assemblages under NTB (Benedetti-Cecchi 2007). The logic behind this is that the NTB makes no specific predictions about the effects of changes in environmental variance. Whilst intensity of disturbance affects the rate of mortality and colonization so that a change in intensity of disturbance may affect species abundance distributions, how disturbance events are arranged in time (equally distributed vs. clustered) should make no difference for assemblages under the assumption of species

equivalence, if intensity of disturbance is kept constant across levels of temporal variance. Thus, changes in environmental variance would not affect the probability of persistence of species under neutrality.

2. Materials and Methods

Assemblages of algae and invertebrates were sampled from 1991 to 2005 every three months on a rocky shore about 1.5 km long at Calafuria (Livorno). Abundances were quantified using non-destructive sampling methods using quadrats ranging in size from 10 x 10 cm to 20 x 20 cm. The size of sampling units was appropriate to sample the small organisms living on the shore and differences in size of quadrats did not affect estimates of mean abundances and variances.

Temporal changes in assemblages were examined using Mantel correlograms based on the Bray-Curtis measure of dissimilarity. To compare observed patterns of temporal change with those predicted by the NTB, assemblages dynamics under the neutral model were generated using the algorithm described in Hubbell (2001, p. 291). Neutral dynamics were based on estimates of parameters obtained by fitting the lZSM distribution to a subset of the observational data from the first two years of study. Simulations were repeated 1000 times to generate confidence intervals around mean values of Mantel's r_s .

To test the hypothesis that a change in temporal variance of disturbance would have no effect on assemblages under neutral dynamics, I compared the fit of the mZSM and lZSM distributions to data originated from an experimental study on disturbance. The details of this study are published elsewhere (Bertocci et al. 2005). Briefly, the experiment consisted in disturbing assemblages in experimental plots (either 50 x 50 or 50 x 100 cm) with a chisel mounted on a battery driller to mimic the mechanical effects of wave shock. The experiment had a factorial design with three levels of temporal variance of disturbance (defined with reference of the interval of time between subsequent events of disturbance) crossed with three levels of intensity (determined by chiselling the plots once, twice or three times) and two levels of spatial extent of disturbance (the two plot sizes). There were three replicate plots in each treatment combination and three unmanipulated plots. The experiment lasted two years (between November 2001 and October 2003); during this period the experimental plots were disturbed six times according to the specific levels of intensity, temporal variance and spatial extent. Plots were sampled seven times during the course of the study using visual counts of abundance of algae and invertebrates. Average values over the seven counts are used in analyses (Benedetti-Cecchi 2003). The hypothesis of interest in the present study is that the same NTB model would fit data from experimental plots that differed with respect to the temporal patterning of disturbance events, but that were exposed to the same overall intensity of disturbance. This hypothesis was tested by comparing the fit of the lZSM and mZSM distributions to unmanipulated data and to data originated from plots exposed to the low, medium and high levels of temporal variance of disturbance (pooling data across levels of intensity and spatial extent of disturbance).

The parameters of the theoretical distributions were estimated using maximum likelihood methods. The lZSM and mZSM distributions were fitted using the analytical

solutions given by Alonso and McKane (2004) assuming an infinite metacommunity. The general solution for a local assemblage of Hubbell's unified theory was given as:

$$S(n) = \theta \int_0^1 P_s(n; J, m, x) \frac{(1-x)^{\theta-1}}{x} dx, \quad (1)$$

where $S(n)$ is the expected number of species with n individuals, θ is the fundamental biodiversity number and $P_s(n; J, m, x)$ is the probability of finding a species with n individuals in a local assemblage of size J with relative abundance x in the metacommunity to which it is connected through the immigration parameter m . The analytical solution for P_s is given as,

$$P_s(n; J, m, x) = \left(\frac{J}{n} \right) \frac{\Gamma(n + \gamma x)}{\Gamma(\gamma x)} \frac{\Gamma(\nu - m)}{\Gamma(\nu - J)} \frac{\Gamma(\lambda + \nu - J)}{\Gamma(\lambda + \nu)}, \quad (2)$$

where Γ is the Gamma function and:

$$\begin{aligned} \lambda &= \gamma x \\ \nu &= J + \gamma(1 - x) \\ \gamma &= \frac{m(J - 1)}{1 - m}. \end{aligned} \quad (3)$$

In the absence of dispersal limitation ($m=1$), Alonso and McKane (2004) give the analytical solution for the metacommunity as:

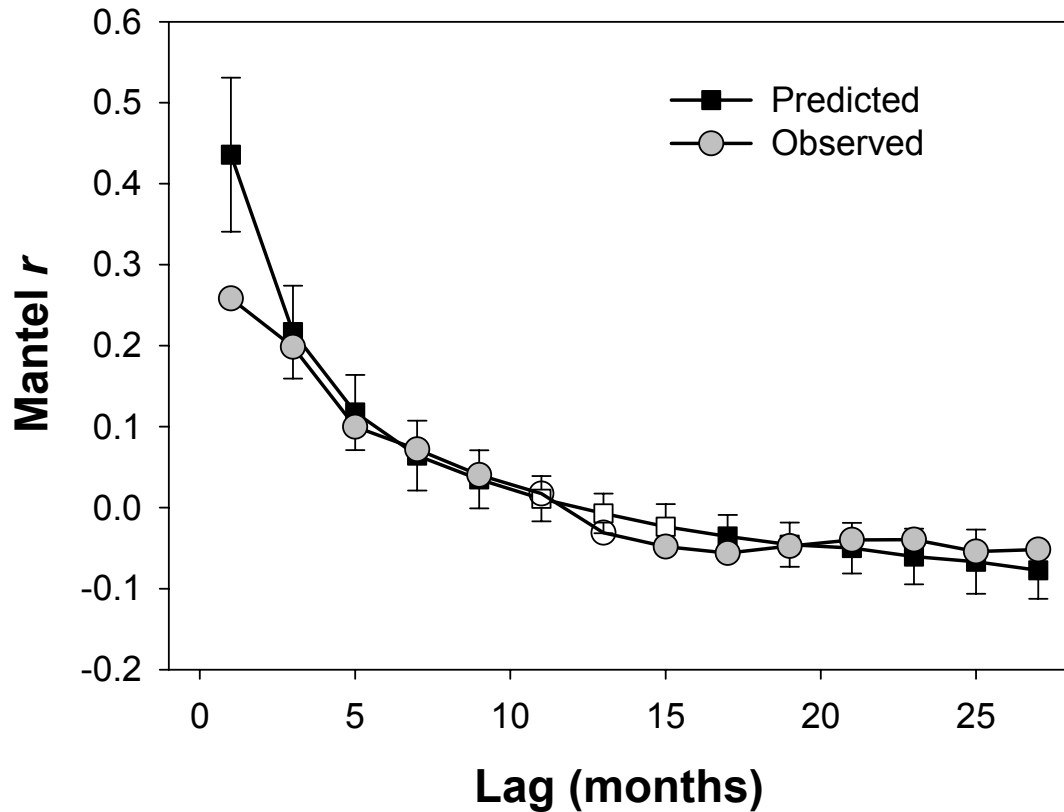
$$S(n) = \frac{\theta}{n} \left(1 - \frac{n}{J} \right)^{\theta-1} + \mathcal{O}\left(\frac{1}{J^2} \right). \quad (4)$$

Fits of the lZSM and mZSM distributions were compared using the AIC criterion (Burnham and Anderson, 1998). All analyses were performed in R using functions `optim`, `optimize` and `integrate` (R Development Core Team, 2004).

3. Results

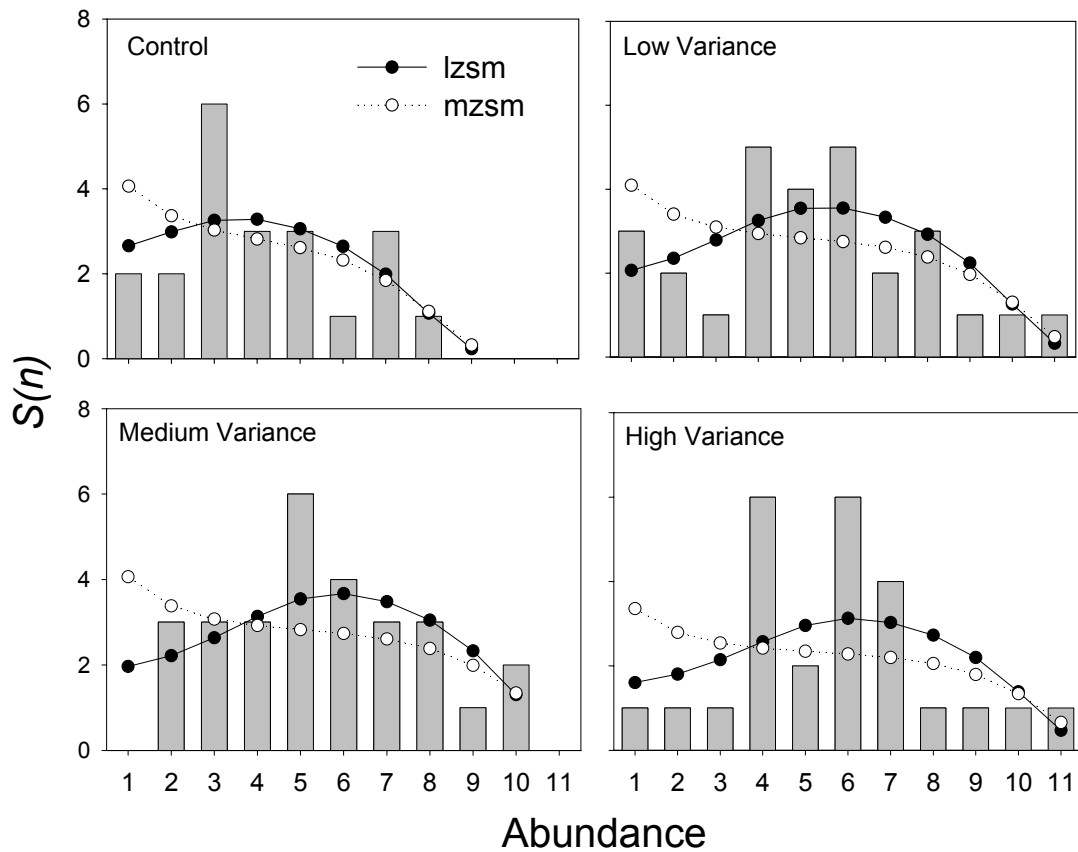
The NTB correctly predicted temporal patterns of decay in similarity for the rocky shore assemblages of Calafuria (Fig. 1). The only exception was the greater similarity predicted by the NTB for the first time lag (3 months).

Figure 1. Comparison of observed patterns of temporal decay in similarity in assemblages of rocky shores with patterns predicted by the NTB. Mantel r 's are based on the Bray-Curtis index of similarity. Error bars for modeled data are 1 standard deviation over 100 replicated simulations. Hollow symbols indicate Mantel's coefficients that do not differ significantly from 0 (significance based on 5000 permutations). Model parameters were $\theta=4.3$ and $m=0.016$. The total number of counts was 1013 and the number of species was 24.



The analysis of the disturbance experiment showed that whilst data from control and low-variance plots were fitted equally well by the two versions of the NTB, data from the medium- and high variance treatments were fitted better by the IZSM than the mZSM distribution (Fig. 2). This was supported by the AIC criterion (for control data: AIC_{IZSM} : 371.4, AIC_{mZSM} : 371.3; for low-variance data: AIC_{IZSM} : 299.3, AIC_{mZSM} : 299.7; for medium-variance data: AIC_{IZSM} : 309.4, AIC_{mZSM} : 313.5; for high-variance data: AIC_{IZSM} : 282.6, AIC_{mZSM} : 286.5). It is interesting to note that under the intermediate level of temporal variance of disturbance, the lowest abundance class is missing, indicating a rare species advantage in this treatment.

Figure 2. Species abundance distributions illustrating the fits of the lZSM and mZSM distributions to experimental data. Abundance categories are based on log2 smooth binning of counts (1, 2, 3-4, 5-8, etc.).



4. Discussion

The results of this study showed that a model of neutral drift correctly predicted temporal patterns of dissimilarity in assemblages at all time scales but the shortest one (3 months), where the NTB predicted less variability than observed. This correlative analysis, however, could not identify neutrality as the true mechanism of change. Alternative explanations can be invoked to explain the gradual change in dissimilarity observed in this rocky shore assemblage. Although ecological drift was expected to produce autocorrelated patterns of change through time, also non-neutral responses of species to autocorrelated environmental processes would be expected to produce the same patterns (Benedetti-Cecchi 2007). In fact, many environmental variables are characterised by red spectra of variability in marine and terrestrial habitats so that spatial or temporal autocorrelation in assemblage structure may reflect this variability (Steele 1985, Vasseur and Yodzis 2004).

The analysis of the experimental data helped clarifying this issue. By changing the level of temporal variance of disturbance it was possible to induce shifts in the species abundance distribution that highlighted non-neutral responses of species to environmental fluctuations. Although very similar AIC values were obtained from fits

of the lZSM and mZSM distributions to control and low-variance data, the first model provided a better description than the second one for the medium- and high-variance treatments. Thus, assemblages experiencing some degree of temporal fluctuations on top of those provided by the natural regime of disturbance, were best described by a model of local community structure that included dispersal limitation. Dispersal limitation, in contrast, was not essential to describe assemblages from control and low-variance treatment. These differences in assemblages related to temporal variance of disturbance would not be expected under neutrality for two main reasons. First, data came from a designed experiment, so the spatial and temporal scales encompassed by the experiment (i.e. distance of replicated plots on the shore and duration) were consistent across treatments. Because each treatment condition combined data from several replicate plots distributed randomly on the shore, the mZSM distribution was expected to fit control and experimental data regardless of levels of temporal variance of disturbance. Second, intensity of disturbance was constant across levels of variance. Thus, according to the NTB, the same patterns of mortality and colonization should have occurred in experimental plots and a single species abundance distribution should have emerged from analyses under the assumption of species equivalence. These expectations were clearly negated by the analysis of the experimental data, indicating that at least some of the species in the assemblage were not equivalent with respect to environmental variance.

These results have important implications for predicting the responses of species and assemblages to increased environmental fluctuations like those expected under climate change (Easterling et al. 2000). Before realistic predictions can be attempted, however, it is necessary to clarify at which scales and for which species neutrality can still be retained as a good approximation of assemblage dynamics. The rare species advantage observed at the intermediate level of temporal variance of disturbance, for example, suggested that these species may not display neutral responses to environmental change, whilst neutrality might be retained for dominant species. Similarly, the discrepancy between observed and predicted patterns of temporal decay in similarity at the shortest time scale suggests that neutrality may not apply at all spatial or temporal scales. Studies on terrestrial vegetation have shown that neutrality may fail to predict assemblage dynamics at very small and very large spatial (Condit et al. 2002) and temporal (Volkov et al. 2005) scales. More focused research on these issues is necessary to combine neutral and non-neutral theory into better predictive models of assemblage dynamics. This is an urgent need, given the increasing frequency and magnitude of environmental changes induced by human activities on natural habitats and assemblages.

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