



## The pattern of species turnover resulting from stochastic population dynamics: The model and field data

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### ABSTRACT

The model of random population dynamics in a sampling site returns geometric distribution of longevities of continuous presence (=persistence) and Poisson distribution of the presence–absence transitions. This discrete-time stochastic process describes the presence–absence pattern observed in the beetles surveyed 6 years on Mount Carmel, Israel. Homogeneous pools of species mostly on the Families rank, exhibit the predicted by the model patterns. Conformity to an ergodic hypothesis is the criterion of ecological homogeneity. This criterion assumes the equivalence of short-term behavior of entire pool and long-term behavior of any species from this pool. The pool of all 801 species of Order Coleoptera does not match the model. Thus a taxon of an arbitrary rank may not be considered a priori as a unit of ecological study. Determined from field data parameters of the model are biased and magnitude of the bias depends on longevity of the survey. Parameter of distribution depends also on species tolerance, which is the level adaptation of given species to given environment in given time interval. Random process of species turnover may be considered as a game of species to gain their presence against deteriorative fluctuations of environmental conditions.

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### 1. Introduction

Many animal species exhibit alternations of periods of their presence and absence in the course of species turnover in a locality. Lists of species change when a multi-species assemblage is surveyed. Frequent observations for a long period in non-isolated sites show that a relatively small proportion of species is recorded during a predominant part of the entire period of observation; more species do not appear frequently. The species of these groups are known as core and satellite (Magurran and Henderson, 2003), resident and tourist (Henderson, 2006), frequent and occasional (Ulrich and Ollik, 2004), respectively. Division of collected species into two groups regarding their occurrence is discussed usually in terms of ecological communities.

A model of dynamics of populations in a sampling site was developed (Vilenkin, 2006). This model describes the stochastic changes of abundance, which are independent of neighboring populations, and it does not contain explicit parameters of a population growth. Assemblages of such populations exhibit the statistical properties assigned usually to biological communities where competition is

presumed. We attempt to investigate species turnover using modified model and some tools of queuing theory. Species turnover may be considered as a game of species to establish presence against odds of the fluctuating environment. Relevant field data are drawn to validate the results. Some features of these data require adoption of a sort of the ergodic hypothesis whose validity is tested in taxa of different ranks. Adoption this hypothesis supposes that a short-term behavior of pooled species shows the same presence–absence pattern as a long-term behavior of any species of the pool.

In this article we explore whether species turnover may be described as the stochastic process. Within the framework of the model, this means that appearances and disappearances of any species in the sampling sites occur by chance and are independent of other species. The model corresponds rather to the null-model (Gotelli and McGill, 2006), and the approach of the study presented may be useful in evaluating the causes of differences between sequential censuses. Description of the model, exploring its behavior under various conditions, and a comparison of the model output with the field data are presented. In this article we determine any group of species as species assemblage, and pool of species is the group of species chosen to test the ergodic hypothesis related to presence–absence alternations. These pools have certain taxonomic rank in our study. Longevity of continuous presence of a species termed persistence (years, time-steps), presence–absence transition termed switch.

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## 2. Materials and methods

Beetles were collected in lower Nahal (=dry summer valley) Oren (32°43'N, 34°58'E) on Mount Carmel, Israel, designated 'Evolution Canyon' (Nevo, 1995). While three sampling sites are at different elevations on each opposite slope of this valley, the seventh sampling site is situated at the valley bottom. Samplings were performed on the same day at all seven sites, usually at intervals of 14 days. Chikatunov et al. (1999, 2004) present the full description of the methods of collection and the beetles' taxonomy. The presence-absence data refer to 1 year and not to shorter intervals because many taxa show the pronounced seasonality. Hence, we are dealing with the discrete-time process. Our database is the Table 801 × 6 containing presence-absence information on 801 species during the years 1995–2000. Numbers of years of persistence are counted in each 6-year interval. Since six time-points are not enough for a statistics, we consider pooled data. The ergodic hypothesis states here that a short-term pattern of presence-absence alternations of all species in the pool is identical to this pattern exhibited by any species from the pool during time equal to (number of pooled species) × 6 years. Ergodic hypothesis opens the way to deal with numerous data on many pooled species instead of considering the 6-year series of every species separately. Adopting this hypothesis assumes ecological identity of all species within the pool. Data are pooled in different ways: for all collected Coleoptera together (801 species), for each of the 16 big families containing 646 species in total, and for some taxa of lower hierarchy as well. We suppose that any species has the possibility to occur every year in the sampling site, and that its success depends on chance. The Poisson process (Cox and Smith, 1971) is expected to describe presence-absence sequences. Switches between these states occur randomly. Numbers of switches at given time intervals should follow the Poisson distribution while persistence should fit the exponential distribution. Geometric distribution is a special case of negative binomial distribution, and it is the discrete equivalent of the exponential model (Cox and Smith, 1971; Johnson et al., 1992). This distribution describes sequences of successes and losses in gambles and thus may be interpreted as a result of game of species against environment. Probabilities of geometric distribution follow the formula:

$$P(\tau) = p(1-p)^{(\tau-1)},$$

$\tau$  is longevity of persistence. Parameter  $p = 1/M$ , where  $M$  is the mean of  $\tau$ -values. Goodness-of-fit of observed in field and/or model distributions is tested using chi-square.

A modification of the basic model (Vilenkin, 2006) generates changes of abundance of a species in a sampling site. Abundance ( $x$ ) is zero at the beginning. The algorithm for returning the value of  $x$  on each next step is:  $x_{t+1} = x_t + \text{rand}(1) - \text{rand}(2)$ , if  $\text{rand}(E) \leq T$ ;  $x_{t+1} = 0$ , if  $\text{rand}(E) > T$  or if  $x_t + \text{rand}(1) - \text{rand}(2) \leq 0$ . The last condition was not involved into the basic model, and it excludes appearance of negative abundances. Here  $\text{rand}(1)$ ,  $\text{rand}(2)$ , and  $\text{rand}(E)$  are evenly distributed between 0 and 1 random numbers changing with every time step.  $\text{Rand}(1)$  and  $\text{rand}(2)$  accumulate effects of birth/immigration and mortality/emigration respectively within boundaries of the chosen sampling site.  $\text{Rand}(E)$  represents environmental fluctuations.  $T$  is the species tolerance that represents the threshold of response of a population to the magnitude of external disturbance.  $0 < T < 1$ . This parameter of a species may be related to the level of adaptation of the given species to a given environment in a given time interval. Physical nature of  $\text{rand}(E)$  may differ among species in an assemblage and change with time depending on species' requirements in this time interval and also on the state of limiting factors of the environment. Value of  $T$  is assigned to every species and does not change in the course of a

run. This model returns positive abundance evaluations only. All non-zero values are transformed to 1 after accomplishing a run. The outcome is a sequence of 0 and 1, where 0 is absence and 1 is presence of a species. This model is compared with field data of beetle species turnover.

Asymptotic behavior of the model in an infinite time is not interesting in our case since published data are restricted to several years (Ulrich and Ollik, 2004) or to couple of tens of years (Magurran and Henderson, 2003). Carabidae with their 87 species is the most species-rich beetles' family, which passes ergodic hypothesis (see below). Six-year survey on 87 species returns equivalent to several hundred years of survey on one species. Hence we must be sure that model produces geometric distributions of persistence in certain range of  $T$ -values in runs up to several hundreds steps. Runs by 10,100 steps at  $0.1 \leq T \leq 0.6$  are done. 700-steps runs are done by  $0.1 \leq T \leq 0.95$ . Data of the first 100 steps are excluded in both the cases due to possibility of some transition process (Vilenkin, 2006). Outputs of each of ten 600-steps effective runs are subdivided into 100 subsamples by 6 steps. Parameter  $p$  of geometric distribution is evaluated for entire 600-steps runs and for pooled subsamples. Poisson distribution of switches in 6-steps intervals is tested.

Conformity of beetle's pool to both testing distributions simultaneously confirms that a stochastic process is running.

## 3. Results

10,000 steps runs fit expected geometric distribution in  $T$ -values range of 0.1–0.6. Tests at higher  $T$  failed. 600-steps runs and their subdivisions fit geometric distributions of persistence in range of 0.1–0.95  $T$ , as well as Poisson distribution of switches. One of two or three trials passes only goodness-of-fit test at  $T$  0.9 and 0.95. The results are shown in Table 1. Evaluations of  $p$  from 10,000 steps runs correlate well with  $T$ -values:

$$p = -0.8526 * T + 1.0207; \quad R^2 = 0.9995.$$

This relation may be presented without a significant loss of accuracy as  $p = 1 - 0.8047 * T$ ,  $R^2 = 0.9956$ .  $T$ - $p$  relation of shorter runs shows a deviation of linearity in the area of big  $T$ -values. Linear approximation is better in transformed coordinates:

$$p = -0.5057 * \exp(T) + 1.4546, \quad R^2 = 0.9956 \text{ (600 steps)}$$

$$\text{and } p = -0.4307 * \exp(T) + 1.3814,$$

$$R^2 = 0.9895 \text{ (pooled 6 steps)}.$$

Difference between two latter regression coefficients is tested using Student's  $t$ -test (Sokal and Rohlf, 1981) and found significant:  $t = 3.18$  at d.f. = 16,  $0.001 < p < 0.01$ . Evaluations of  $p$  from pooled 6-steps sequences are biased relatively those of respective entire 600-steps sequences. This bias may be corrected:

$$p(600) = 1.1696 * p(6) - 0.1640, \quad R^2 = 0.9966,$$

and the above relation is using for evaluation non-biased  $p$ -values of the pools of species shown in Table 2. We could obtain somewhat different relationships among outputs of repetitive runs but main tendencies remain similar to shown above. Table 2 contains parameters of geometric and Poisson distributions, which fit the beetles' censuses. The species are pooled at Family level and at level of Order Coleoptera. Data of each pool are considered as presenting one sequence of longevity equals (species number) × 6 years. Tests failed in all beetles unified and in two families. These families seem heterogeneous since Genus Longitarsus of Chrysomelidae passes the test as well as a part of Coccinellidae does this. A pronounced excess of species number with persistency of 4–6 years in almost all families and all beetles together is well seen. Fig. 1 exemplifies this in Scarabaeidea Family.

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