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Bio-Demographic Aspects of Population Entropy in Quantifying Population Heterogeneity and Its Consequences for Population Fitness and Species Adaptation

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Abstract: Entropy is a well-established measure of population variability and already used in contingency in life table analysis to capture the trends of population heterogeneity. However, entropy has been also utilized as a more general dynamic measure of species fitness and adaptation to varying ecological conditions. In this study we are concerned with a brief account of the latter. In principle, such demographic-population entropy is an analogue of the Gibbs–Boltzmann entropy in statistical mechanics, $H=-\Sigma p_i \ln p_i$. Here, p_i represents the probability density function of the age of reproducing individuals and therefore maximization of entropy is equivalent to maximization of the uncertainty of age reproduction. Moreover, considering that demographic dynamics are formally equivalent to the dynamics of a Markov chain, demographic entropy may be used to estimate the convergence rate of insect population transitions to the stable age distributions and demographic equilibriums under certain conditions. By interpreting population entropy as a distance measure between the variability of the mortality distribution where no outside forces interfere and the conditional entropy estimated given the known unperturbed reference mortality we may quantify species adaptive value. Through this operation, populations with the favored demographic properties gradually develop fitness advantages in the presence of the artificial selection factor.

Keywords: population entropy; fitness; adaptation; equilibrium

1. Introduction

Speciation is the outcome of two major factors, variation and selection. The first one can introduce new variability within a population; whiles the second, defines which of the new combinations are able to follow to the next generations through competition for available resources. Both elements can be stated in terms of the species intrinsic rate of increment.

The hierarchical properties of Entropy and the close related mutual information, have been regularly used as general measures as the basis for making theoretical predictions of genetic diversity based on models of population dynamics, which can be tested experimentally and in the field. By using the principle of Maximum Entropy for instance, one make efforts to predict the patterns of ecological species diversity from local to global scales [1].

Nevertheless, in an effort to quantify the species' capacity of increase and pull in some evolutionary extensions and interpretations [2, 3] Demetrius introduced demographic entropy as measure species adaptation and founded the directionality theory. In brief, the concept invokes the fundamental attributes of demographic entropy, as a measure of Darwinian fitness of age structured populations, to study the changes in genotypic and phenotypic composition as generated by the mutation-selection regime [4].Furthermore, established along the Leslie model Tuljapulkar [5], proposed a shift of the Leslie population model, to be patterned as a Markov chain in discrete time, in parliamentary procedure to quantify population converges to its stable age distribution [5, 6]. By such a context demographic entropy has been used by Damos [7] as a highly qualitative predictor of the species survivorship budged and net reproductive success of insect populations reared in different temperature conditions towards the stable age distribution.

The later approach includes the use of entropy (i.e. population entropy) utilized as an inference technique to measure the force of extraneous constituents on the uncertainty in ensemble predictions of age structured populations [7], in contrast to the Maximum Entropy principle which is used as statistical tool to quantify species biodiversity [1]. As in the case of statistical quantum mechanics and machine failure theory, in which information entropy is related to the uncertainty of the realisation of a random variable, demographic entropy is close related to the average probability of the species survivorship function. The shape and limiting behavior of the later enclose information upon population response and its robustness to perturbations. From a theoretical standpoint, such responses significantly modify gene flow and phenotypic expressions through the next generations having important evolutionary consequences.

In this work we are mostly interested in using population entropy in describing age transitions in poikilothermic organisms, namely insects and related arthropods, as moved by an outside factor such as pesticides application which affects the initial conditions of the age structure. The interest is to examine whether demographic fitness and convergence rate to demographic equilibrium may be affected by the use of a pesticide and the extent to which this relation affects transitions rates to the stable age distribution after the perturbation. A short example is given.

2. Results and Discussion

2.1 Demographic entropy as summary statistic and species adaptive value

Demetrius (1974) [8] brought out the concept of population entropy *H* as a summary statistic to define species fitness. In practical terms the maximization of population entropy *H* under various constraints yields to distributions of reproduction and survivorship [2, 3, 4].
By considering that l_x stands for the probability that an individual born at age zero survives to age *x*, and that m_x is the age-specific fecundity of cohort life table, equations and R_0 the net reproductive rate, and so the population entropy can be derived as [8]:

$$H = -\int_0^\infty q(x)\log q(x)dx \tag{1}$$

where:

$$q(x) = \frac{l_x m_x}{R_0} \tag{2}$$

is the probability density function of the age of reproducing individuals. The net reproductive rate (R_o), If $l_x m_x$ is the net maternity function and for fixed $m_x=1$, then

$$H = -\int_0^\infty \frac{l_x}{e_0}\log q\frac{l_x}{e_0}dx = -\frac{\int_0^\infty l_x \log l_x dx}{\int_0^\infty l_x dx} + \log e_0 \tag{3}$$

Where e_0 is the life expectancy

$$e_0 = \int_0^\infty l_x dx \tag{4}$$

Moreover, if we define the normalised entropy H^* as

$$H^* = -\frac{\int_0^\infty l_x \log l_x dx}{\int_0^\infty l_x dx} \tag{5}$$

Then one can define two entropy's [2]: the first one, H^*, corresponds to the population in cases where no environmental forces interfere and the second one, H', consist of the conditional entropy, which is addressed to a perturbed population related entropy given that unperturbed mortality is known.
The relation:

$$\psi = H^* + H' \tag{6}$$

consist of the adaptive value of a given population and can be interpreted as measure of correlation between the variability of the mortality distribution and environmental variability [8].

Equation (*5*) can be regarded as an analogue of the Boltzmann–Gibbs definition of the entropy of a thermodynamic system. The numerator is analogous to the Shannon–Weaver measure of the amount of information in a message; it measures the variability of the contribution of different age classes to the stationary population. Since mutation introduces new types and affects population age patterns and its reproductive performance (e.g. demographic parameters) the interaction between ancestral and mutant types drives the population to some new equilibrium. Global changes in entropy, when moving from the one equilibrium state to the next consist of the adaptive value of the population and in the frame of the directionality theory, population entropy is maximized in equilibrium species and minimized in opportunistic species [4, 9]. From a pragmatic standpoint, population entropy may be applied as a standard to measure heterogeneity of insect population in relation to different external conditions that change the conformation of the initial age structure of a population [7]. From an information theoretical standpoint, where entropy is referred to as a measure of information, minimizing *H* yields minimum uncertainty (high information and population stability), and while maximum *H* represents maximum uncertainty (low information and population stability).

2.2 Matrix models and dynamic population entropy in terms of Markov chains

Let n_x be the number of organism (e.g. Insect) in age *x* (or stage for stage structured models) at time *t*. S_x is the survival of the cohort in age interval *x* to *x+1* and m_x corresponds to the average number of female offspring per female in age interval *x* to *x+1* [7, 10, 11]. These amounts are related as follows:

$$n_{x+1,\tau+1} = n_{x,\tau} S_x \tag{7}$$

and

$$n_{0,\tau+1} = \sum_{x=0}^{n} n_{x,\tau} m_x = n_{0,\tau} m_0 + n_{1,\tau} m_1 + n_{2,\tau} m_2 + \ldots \tag{8}$$

Equations (6) and (7) can be combined according to the following projection scheme:

$$\begin{pmatrix} m_0 & m_0 & m_1 \ldots\ldots\ldots\ldots m_{i-1} \\ S_0 & 0 & 0 \ldots\ldots\ldots\ldots\ldots 0 \\ 0 & S_1 & 0 \ldots\ldots\ldots\ldots\ldots 0 \\ . & & \\ 0 & 0 & 0 \ldots\ldots\ldots\ldots 0 \end{pmatrix} \begin{pmatrix} n_0 \\ \\ n_1 \\ n_2 \\ . \\ . \\ n_{i-1} \end{pmatrix}_{\tau} = \begin{pmatrix} n_0 \\ \\ n_1 \\ n_2 \\ . \\ . \\ n_{i-1} \end{pmatrix}_{\tau+1} \tag{9}$$

If we denote by upper case bold faced symbols as Matrices (e.g., ***L*** for the Leslie model) and vectors (e.g. ***N*** for the number of organisms); vectors are column vectors by default. Hence, by utilizing the traditional Leslie matrix population model as starting point, which is a distinct (or finite) model one can further represent using matrix notations according to the following projection scheme:

$$\boldsymbol{N}_{(t+1)}=\boldsymbol{L}\boldsymbol{N}_t \tag{10}$$

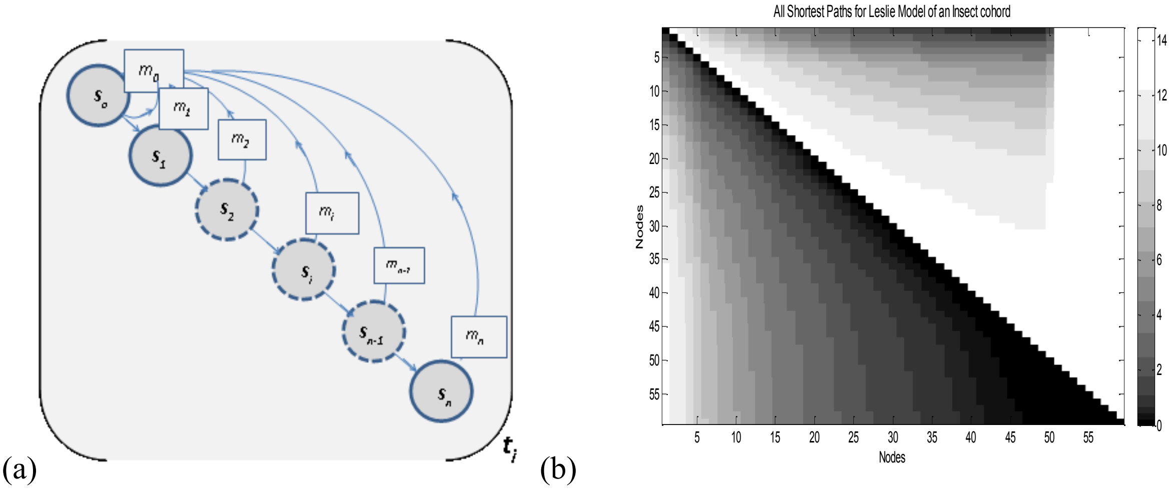
were n_t is the population vector at time t and **L** is the Leslie matrix. If we denote by upper case bold faced symbols as Matrices (e.g., ***M***) and vectors (e.g. ***N***); vectors are column vectors by default.

The Leslie equation (*10*) can be replaced by the following equivalent Markov chain [5] which satisfy the Markovian properties:

$$p_i^{(t+1)} = P_L \; p_i^{(t)} \tag{11}$$

Where, p_i represents probabilities being at particular age category at time t, and P_L is the stochastic transition matrix (i.e. each row adds to 1) that associates the transition from any state to any other state. Concluding, with any Leslie model is associated a graph (Figure 1). The Leslie model may be further transformed to satisfy the Markov assumption and be treated as a Markov chain. The state space S is the set of all possible states in which system can be with respect to its time evolution and arrows represent state transitions having certain probabilities.

Figure 1. (**a**) Abstract representation of the Leslie model for a population cohort in terms of directed graph. The Leslie model is very similar to a discrete-time Markov chain that treats the demographic categories of the projection system as states of the state space. (**b**) All shortest paths of a Leslie model for a representative age structured insect cohort. Adjacency matrix permits transitions between age classes (here: 59x59) with ''forward'' (S_i) and ''backward'' (m_i) Markov transitions.



2.3. Convergence rates of population entropy towards equilibrium

With the above probability scheme, one can further estimate the Markovian entropy $\boldsymbol{H}$ [6] which equals the average uncertainty of the system for moving one step ahead when starting with one given initial state S_i.

$$H_i = -\sum_{j=1}^{n} p_{ij} \log p_{ij} \tag{12}$$

where p_{ij} stands for the probability of any one of a discrete chain moving from the ith to the jth state. Therefore, in comparison to Demographic entropy as a statistical standard measure, the Markovian entropy has dynamical meaning since it touches the average uncertainty of the system for moving one step forward when starting with one given initial state [12]:

$$H_i = -\sum_{j=1}^{n} p_{ij}{}^{r} \log p_{ij}{}^{r} \tag{13}$$

More generally, the set of events of going from S_i to any other state in r steps constitutes a finite complete probability scheme with entropy:

$$H_i = -\sum_{j=1}^{n} p_{ij} \log p_{ij} \tag{14}$$

where p_{ij} stands for the probability of any one of a discrete chain moving from the *i*th to the *j*th state in *r* steps. Thus, the entropy of the chain for moving *r* steps ahead from the initial states when the initial probabilities are specified is:

$$H^r = \overline{H}_i^{\,r} = -\sum_{i=1}^{n} p_i H_i^{\,r} = -\sum_{i=1}^{n}\sum_{j=1}^{n} p_i p_{ij}^{\;r} \log p_{ij}^{\;r} \tag{15}$$

Thus it expected that the average entropy for different population's to convergence by different rates and effect their robustness to factors that affect their initial age structure.

2.4. Mixing times of population entropy towards equilibrium

To argue the time point of the projection scheme where entropy and information loss do not shift dramatically between populations that converge by different modes, the velocity of the process can be brought out as follows:

$$\bar{\upsilon} = \lim_{\Delta t \to 0} \frac{\mathrm{p}_{(\mathrm{i}+\Delta t)} - p_{(i)}}{\Delta t} \tag{16}$$

while the respective mixing rates are now:

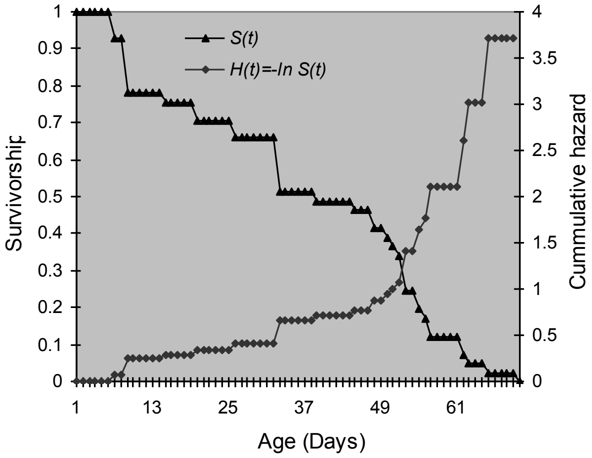
$$\bar{r} = \frac{1}{\bar{\upsilon}} \Delta t \tag{17}$$

Where Δ_t are increments, which matches to each time step ahead. Nevertheless, analysis, mixing rate towards equilibrium probability can be also estimated using other distance measures as well [7].

3. Experimental Section

Since the life table is similar to the statistical reliability theory, in the sense that life is viewed as a random experiment and survival and death is randomly subject to change, it has been used to longevity studies [11]. The life table can be thought of as an "enhanced" frequency distribution table and in this context species specific death risk and how it is altered in relation to aging can be described in terms of reliability theory. In general one can address a demographic entropy to the distribution of survival times, which are expressed in terms of survivorship functions [*S (t)*], the respective probability density function [*f (t)*] and the hazard functions [*h (t)*] (Figure 2).

Figure 2. (**a**) Survivorship function (S_x) and cumulative hazard (H_t) that describes age dependent survival for a typical insect population that has been maintained at constant conditions (i.e. 26±1°C, 16:8h L:D).



There are four types of survivorship curves [8, 13] in which in type *I* mortality occurs in the older population, in type *II* a constant number of individuals dies per unit time, in type *III* the proportion dying per unit time is invariant, and in type *IV* most of the death rate occurs in the early levels, the latest is typical of field populations of insects [15]. In summation, since a certain probability function exists statistical entropy can be directly addressed to the survivorship function of the species of interest.

Figure 3 shows the relative analogies between the intrinsic rate of increase and demographic entropy for five populations reared under different temperature conditions. The intrinsic rate of increase and population entropy summarizes different biologically significant consequences of age-specific schedules of mortality and fecundity. One advantage of population entropy over the intrinsic rate of increase is that it is related to the rate of decay of population fluctuations and thereby provides a precise measure of demographic stability [5, 6].

Figure 3. (**a**) Some typical effects of temperatures (°C) intrinsic rate of increase, *r*, of insects. The intrinsic rate of increase considered by most as the demographic statistic that captures the fitness of a population. (**b**) Typical effects of temperature on the demographic entropy, *H*, of an insect. Values impose constraints on the shape of the net-reproductive function and represent the species demographic heterogeneity accrues from life table analysis [10]. These values represent the variability of the contribution of different age classes to the stationary population.

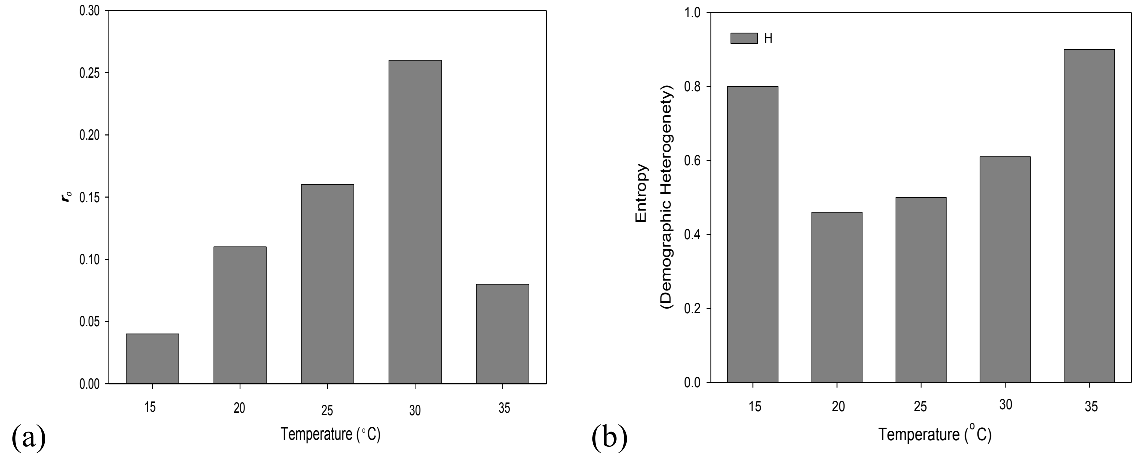


Figure 4 depicts the probability convergence towards equilibrium of two hypothetical populations that have three age classes and how the age structure and convergence to equilibrium of the treated population is affected by an external stress factor. These demographic properties do constrain the rate of which species adapt to human disturbed environments. Repeated use of pesticides for instance can cause undesirable changes in the gene pool due to artificial selection. Through this process, the population gradually develops resistance to the pesticide and detection of resistance individuals usually show fitness disadvantages in the absence of the artificial selection factor [15, 16].

Figure 4. Generated Markov chain model that corresponds to an initial transition probability matrix scheme having three states – age classes (S1, S2, and S3) and convergences to the limiting probability in respect to external disturbances that affect initial conditions of the age structure (stress factor scheme) and reference population (reference). Note that the action of an external factor which affects the age-specific vital rates affects the final population size and age structure towards equilibrium which differs greatly between the two populations.

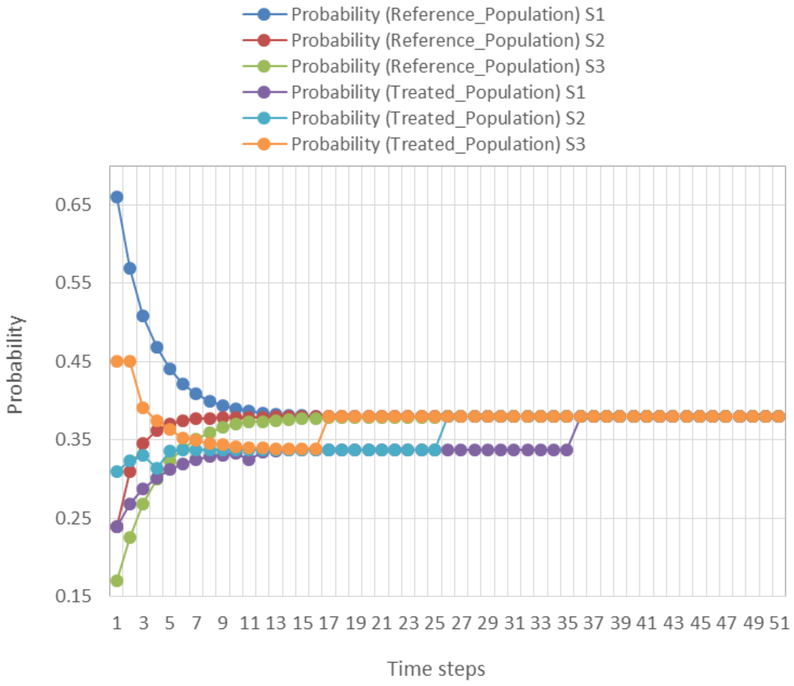


Figure 5 depicts deviation of entropy convergence from entropy at equilibrium, for a reference population cohort (right) and that which has experienced a stress factor (left), while Figure 6, shows the mixing times towards demographic equilibrium. Note again that mixing times differ significantly between the reference population cohort and that of the treated cohort which has experienced the stress factor.

Figure 5. Population entropy convergences of the Leslie projection scheme for two hypothetical insect population cohorts with three age classes, modeled as an exact Markov chain. Note that population entropy convergence at different rates and distances in regard to entropy at demographic equilibrium for a reference population cohort (right) and that which has experienced a stress factor (left). The stress factor may correspond to the treatment with certain pesticide which has modified the initial conditions in the probability transition matrix.

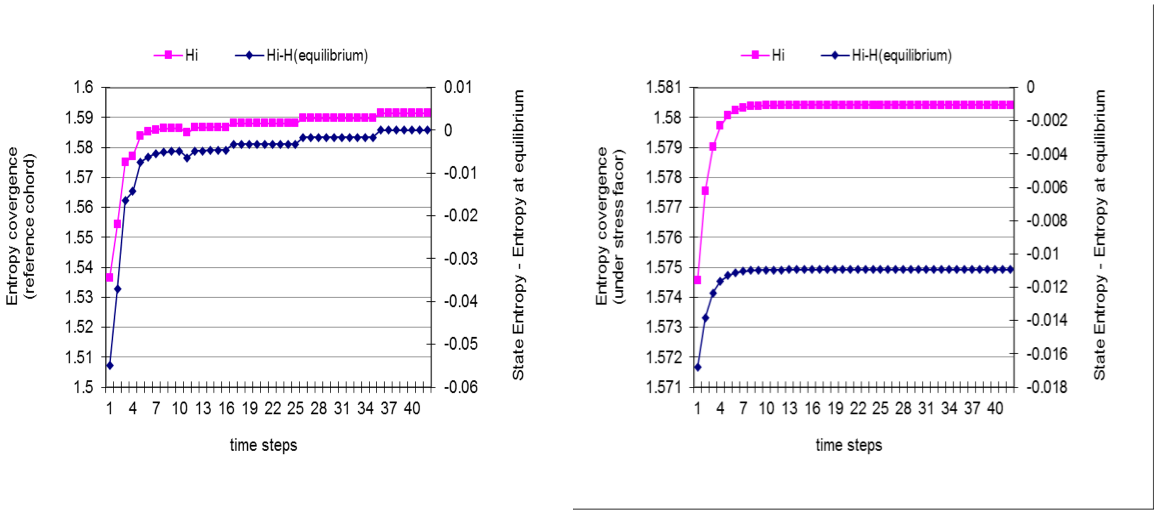
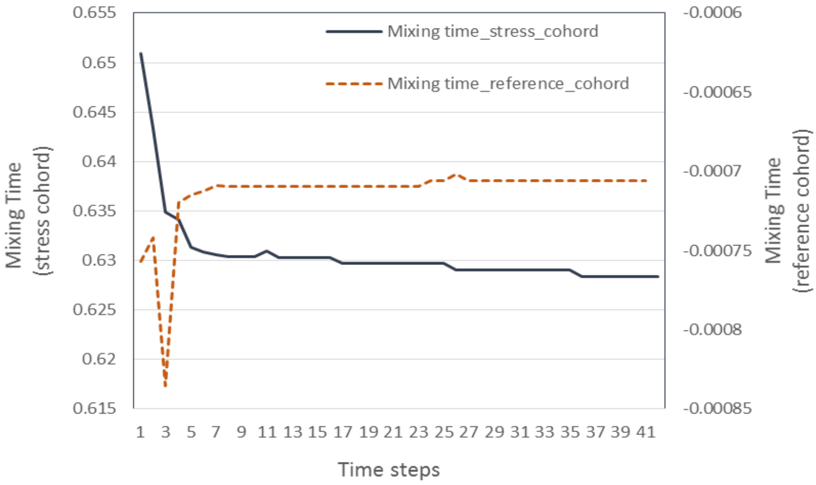


Figure 6. Mixing times towards demographic equilibrium of the Leslie projection scheme for two hypothetical insect population cohorts with three age classes modeled as an exact Markov chain. Note that mixing times differ significantly between the reference population cohort and the cohort which has experienced a stress factor. As previously, the stress factor may correspond to the treatment with certain pesticide which has modified the initial conditions if the probability transition matrix.



3. Conclusions

Equations (*5*) and (*12*) can be seen as an analog of the Boltzmann–Gibbs definition of the randomness of a thermodynamic system. In equation (*5*) the numerator is analogous to the Shannon–Weaver measure of the amount of information in a message; it measures the variability of the contribution of different age classes of the stationary population.

Since mutation introduces new types and affects population age patterns and its reproductive performance (e.g. demographic parameters) the interaction between ancestral and mutant types drives the population to some new equilibrium. Global changes in entropy, when moving from the one equilibrium state to the next consist of the adaptive value of the population and in the frame of the directionality theory, population entropy is maximized in equilibrium species and minimized in opportunistic species [8].

As shown population entropy numerical studies should be thus profitable in population studies in cases in which we want to determine the rate of convergence to equilibrium in situations where several activities and factors disrupt the initial population stability. This information is also important to predict colonization dynamics and/or species invading potentials for new areas and simulating life history evolution [16, 17]. In a population with shorter generations for instance, it’s important to evolve relatively fast per generation to adapt to given rates of environmental changes (e.g. artificial selection and pesticides resistance), while species with low intrinsic rate of increase will reach extinction quite faster since they cannot adapt to abrupt and fast environmental changes [16, 17].

Concluding, for a given species, fitness and reproductive performance are a function of the environment and the diversion of the mean demographic properties can measure how fast genetic shift occurs. Emanations of these transactions could be expressed through the evolution of new phenotypes and/or strains having variants life traits [18]. This plasticity is a direct impact of the environment on the development of successful phenotypes, which apart of morphological diversity involves also the development of physiological, behavioral and demographic responses [19]. The degree of phenotypic expression, here population entropy, depends upon the species intrinsic factors, the time scale of exposition and the intensity of the selective factor. Under an evolutionary perspective the genetic variance as a product of phenotypic variation and heritability, drives evolution and allows persistence of individuals to new conditions.

Conflicts of Interest

“The author declare no conflict of interest”.

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