Fuzzy subset approach in coupled population dynamics of blowflies

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ABSTRACT

This paper is a study on the population dynamics of blowflies employing a density-dependent, non-linear mathematical model and a coupled population formalism. In this study, we investigated the coupled population dynamics applying fuzzy subsets to model the population trajectory, analyzing demographic parameters such as fecundity, survival, and migration. The main results suggest different possibilities in terms of dynamic behavior produced by migration in coupled populations between distinct environments and the rescue effect generated by the connection between populations. It was possible to conclude that environmental heterogeneity can play an important role in blowfly metapopulation systems. The implications of these results for population dynamics of blowflies are discussed.

Key terms: Fuzzy logic, blowflies, coupled populations, population biology.

INTRODUCTION

A central goal in population biology is to understand temporal fluctuations in population abundance (Berryman, 1999). Such fluctuations, however, often exhibit apparently cyclic population behavior or more complex dynamic expressed by erratic and random oscillations (May, 1974; Cushing et al. 2003). Levels of variation may range from small percentages to several orders of magnitude when analyzed with deterministic or stochastic models or even if directly investigated from empirical data (Renshaw, 1999; Cushing et al., 2003).

The description of deterministic complex dynamics in population models has received special attention in recent years because it has indicated surprising effects on the understanding of several biological processes (May, 1974, 1975, 1995). High growth rate values may lead theoretical populations to cyclically or unpredictably fluctuate (May, 1974; Godoy et al., 2001). Thus, fluctuations in population size can be chaotic, that is, apparently random but, in fact, strictly deterministic. However, fluctuations in population size are extremely sensitive to initial conditions; minute differences in initial x values (x_n) lead to very large differences in future population fluctuations, which makes predictions impossible (Edelstein-Keshet, 1988).

In addition to these conclusions about population dynamics, Renshaw (1991) advocates full recognition that the environment has a spatial dimension, since individual population members rarely mix homogeneously over the territory available to them but develop within separate subregions. Subsequent interaction between these subregions, whether in the form of migration

of individuals or cross-infection of disease, can vary from purely local to involving the entire area studied (Turchin, 1998).

Despite the great importance of these findings, several models assume that populations are homogeneous, comprised of individuals all interacting with one another, which would justify the use of average *r*-values for whole populations. Nevertheless, it is possible that many local populations differ in their growth rates, since the environments are likely heterogeneous (Hanski, 1999; Harrison and Taylor, 1997; Godoy and Costa, 2005).

An understanding of the processes leading to population fluctuations in a metapopulational context with environmental heterogeneity, as well as persistence and/or extinction, is relevant to many questions in population biology, such as life history evolution, the success of colonizing species, and the management of endangered species and zoo populations (Hanski, 1999). The causes of extinction may be related to several factors: demographic processes, such as random fluctuations in birth and death rates and sex ratio; seasonal and other changes in the environment, including predation and competition; catastrophes, disease outbreaks, and genetic problems, including the accumulation of deleterious mutations or the loss of adaptive variation (Lawton and May, 1996).

Traditional approaches to mathematical modeling applied to population dynamics and risks of extinction require advanced mathematical skills, principally because populations tend to fluctuate as a function of their variability in demographic parameters (Gotelli, 1995; Godoy and Costa, 2005). This is why, when studying animal behavior, many mathematical models actually are presented by mathematicians rather than ethologists or ecologists. But even when the researchers cannot produce a mathematical model directly, they might be able to describe the system and its behavior linguistically (Barros et al., 2000). In this sense, the question would be: how can we transform linguistic observations into mathematical components in order to analyze dynamic behavior patterns and/or susceptibility to local or global extinction?

Krivan and Colombo (1998) developed a non-stochastic methodology to deal with the uncertainty in models of population dynamics, including a fuzzy approach. Although a stochastic approach led to a number of useful results (May, 1974; Turelli, 1986), there also is some criticism concerning its appropriateness in models of population biology. This criticism is related mainly to the fact that particular noises are mathematical frameworks which, though a reasonable model in physics and electronics, may not be a suitable description of disturbances in biological systems (Steele, 1985; Halley, 1996).

The concepts of fuzzy set and fuzzy logic were introduced by Zadeh (1965). Zadeh was working in the field of control engineering. His intention, when introducing this theory, was to deal with problems involving knowledge expressed in vague, linguistic terms. Classically, a set is defined by its members. An object may be either a member or a non-member, the characteristic of a traditional crisp set. The connected logical proposition also may be true or false. This concept of crisp set may be extended to the notion of a fuzzy set with the introduction of the idea of partial truth. Any object may be a member of a set "to some degree," and a logical proposition may be true "to some degree" (Bezdek, 1993).

Fuzzy modeling is the most effective approach to transform linguistic data into mathematical formulas and vice versa. Indeed, Dubois and Prade (1998) state that the real power of fuzzy logic lies in its ability to combine modeling (constructing a function that accurately mimics given data) and abstracting knowledge from the data. Fuzzy theory is also an alternative approach to study population changes, since it allows fractional membership in multiple clusters, making many forms of biological organization more realistic (Schaefer and Wilson, 2002). A fuzzy set admits gradation between established boundaries and provides a graphic description that expresses how the transition from one to another takes place.

This paper is a comparative study about the population dynamics of exotic and native blowflies, employing a non-linear

mathematical model for population growth (Prout and McChesney, 1985) connected to a coupled population formalism (Roughgarden, 1998) that incorporates fuzzy logic. We believe that a fuzzy approach relates to the empirical and philosophical foundations of our principal concern, which can be expressed by a question. How can environmental variability affect the dynamic behavior in coupled populations of *L. eximia,* a neartic and neotropical blowfly species (Prado and Guimarães, 1982, Madeira et al., 1989) and *C. albiceps,* an exotic species introduced into the Americas about thirty years ago (Guimarães et al. 1978, 1979)?

The objective of this paper is to investigate the coupled population dynamics of the blowfly by applying fuzzy subsets to model population trajectory, considering different environmental quality levels, and by analyzing demographic parameters, such as fecundity, survival, and migration.

MATERIAL AND METHODS

Laboratory populations of *L. eximia* and *C. albiceps* were used (Godoy et al. 2001, Silva et al. 2003). The trials were carried out using F_2, the progeny of one generation that had completed its life cycle in the laboratory. Exploitative intraspecific competition among immatures of *L. eximia* and *C. albiceps*, which is known to occur under natural conditions, was established in the laboratory. The experimental setting was designed to evaluate at least five larval densities, 100, 200, 400, 600, 800 larvae per vial (7.2 cm by 13.8 cm), with two replicates for each density. Fecundity (Table I) was measured by counting the number of eggs per female and expressed as average daily egg output, based on the length of the gonotrophic cycle at 25°C (Linhares, 1988). Survival was estimated as the number of adults emerging per vial and as a function of the larval densities (Table I).

TABLE I

Mean daily fecundity and survival in larval densities

Density	Survival		Fecundity		
	n	Mean	*n*	Mean	sd
L. eximia					
100	2	91.5	32	6.53	1.11
200	2	84	32	7.03	1.58
400	2	59	32	6.14	1.21
600	2	38	31	5.29	0.55
800	2	36	32	4.05	0.71
C. albiceps					
100	2	54	25	26.46	4.13
200	2	34	54	21.02	2.96
400	2	12	29	19.24	2.97
600	2	7.2	17	15.91	3.15
800	2	6.9	22	13.63	2.87
1,000	2	2	10	8.57	2.43

Mathematical models

The mathematical model developed by Prout and McChesney (1985), a standard function of density-dependence, was used to investigate the dynamics of laboratory populations of *L. eximia* and *C. albiceps* by applying a fuzzy coupled-population approach. The density dependent model is based on a finite difference equation, and the population dynamics is based on the number of immatures, eggs or larvae, in succeeding generations, n_{t+1} and n_t. It incorporates two density-dependent processes, namely, the variation in fecundity (F) and survival (S), as a function of the density of immature forms, n_t. The recursion is expressed by a non-linear finite difference equation, written as:

$$n_{t+1} = \frac{1}{2} F^* S^* e^{-(f+s)n_t} n_t \qquad (1),$$

where F^* and S^* are the intercepts in the exponential regression analysis of fecundity and survival as a function of larval density (Table II). These parameters describe the theoretical values for maximum fecundity and survival, respectively. The factor $^1/_2$ indicates that only half of the population consists of adult females that contribute eggs to the next generation. The values of f and s are regression coefficients that estimate the effect of slope of fecundity and survival on the density of immatures (Table II).

TABLE II

Parameters for the regression analysis of fecundity and survival on larval densities

Lucilia eximia	FECUNDITY	SURVIVAL
Intercept in *y*	9.08	1
Regression coefficient	0.01	0.0014
t value	77.3	0.94
r²	0.6517	0.92
ANOVA	296.64	115.71
Chrysomya albiceps	FECUNDITY	SURVIVAL
Intercept in *y*	27.11	0.565
Regression coefficient	1×10^{-3}	3×10^{-3}
t value	18.36*	5.48*
r²	68.5	75
ANOVA	337*	30*

* P < 0.001

The exponential function was used because it fitted the blowfly data as well as or even better than the linear and hyperbolic functions. In addition, linear regression produces larger slopes (in absolute magnitude), which in turn, produce larger eigenvalues that do not accurately describe the model dynamics at carrying capacity (Mueller 1985). Furthermore, the decrease in fecundity as a function of the density of immatures can be viewed biologically as a Poisson process described by an exponential function (Rodríguez, 1989).

The model for two coupled populations can be written as

$$n_{1,t+1} = r_{1,t} \left[(1-m)n_{1,t} + mn_{2,t} \right]$$

$$\qquad (2).$$

$$n_{2,t+1} = r_{2,t} \left[mn_{1,t} + (1-m)n_{2,t} \right]$$

In this model, m is the probability that an organism from subpopulation 1 disperses to subpopulation 2 and vice versa, i.e., it is the probability that an organism will migrate (Roughgarden, 1998). Therefore, (1-m) is the probability that an organism will remain in its original patch and will not migrate to another patch. The term $n_{x,t}$ is the number of individuals in the population at time t and location x, where x is 1 or 2. The geometric growth rate at location x at time t is r. If m is zero, the equations describe two separate uncoupled populations, and if m is $^1/_2$, the two populations are completely mixed and are actually one population. Combining Prout and McChesney (1985) and coupled population equations yields

$$n_{1,t+1} = \left[(1-m_1)\tfrac{1}{2}F_1^* S_1^* e^{-(f+s)n_t} n_t + m_2 \tfrac{1}{2} F_2^* S_2^* e^{-(f+s)n_t} n_t \right]$$

$$\qquad (3).$$

$$n_{2,t+1} = \left[m_1 \tfrac{1}{2}F_1^* S_1^* e^{-(f+s)n_t} n_t + (1-m_2)\tfrac{1}{2} F_2^* S_2^* e^{-(f+s)n_t} n_t \right]$$

In this model, the geometric growth rate (r) was removed in order to introduce the demographic parameters of fecundity (F) and survival (S), which are functions of the larval density. The parameters F, S and m are conventionally known for their great density dependence, associated with resource

availability and environmental factors (Prout and McChesney, 1985; Godoy et al. 1997). Hence, in this study they were considered linguistic variables and therefore estimated using fuzzy rules. Figure 1 describes the components of a system based on fuzzy rules (Pedrycz and Gomide 1998).
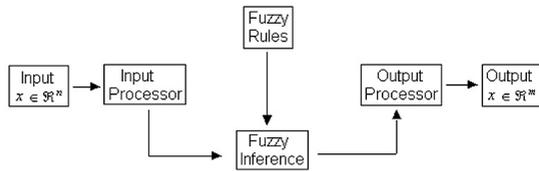

Figure 1: Framework of systems based on fuzzy rules.

Inputs of the system are the linguistic variables Populations and Environment. Then the linguistic terms were attributed to them: populations were classified as small,

medium, and large; and environment as hostile, slightly unfavorable, and favorable. Fecundity and survival were classified as low, moderate and high. These terms were modeled mathematically by fuzzy sets in their respective domains according to the figures 2 A, B, C and D. Fecundity and survival were modeled with maximum and minimum values experimentally obtained for each species (Table 1). Migration was modeled according to Figure 3 at domain [0, 1].

The fuzzy rules, which incorporated a set of premises written as "*if – then*" can be described as follows:

If the population is small and the environment favorable *then* the fecundity and survival are high and the migration low.

If the population is small and the environment slightly unfavorable *then* the fecundity is high, the survival medium, and the migration low.
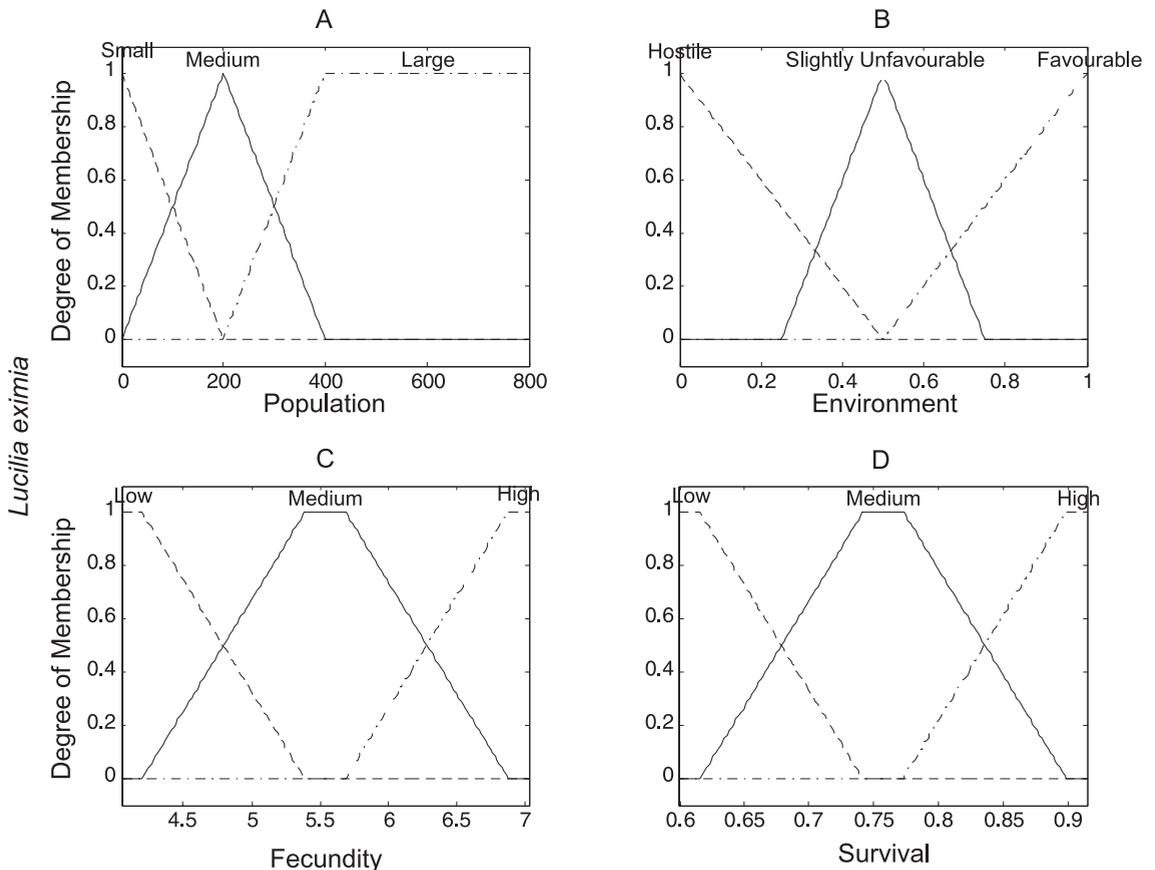

Figure 2: A. Population, B. Environment, C. Fecundity and D. Survival for blowflies.
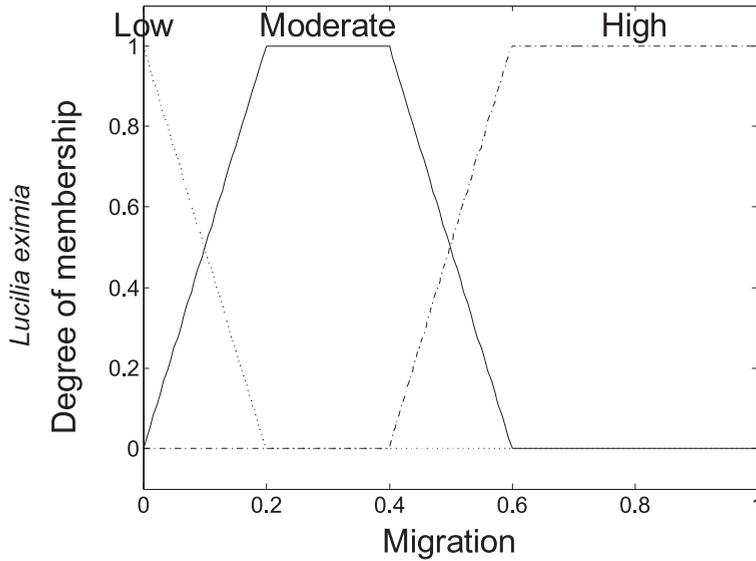
Figure 3: Migration of blowflies (high, low, moderate).

If the population is small and the environment hostile *then* the fecundity is medium, the survival low, and the migration high.

If the population is medium and the environment if favorable *then* the fecundity is high, the survival medium, and the migration low.

If the population is medium and the environment slightly unfavorable *then* the fecundity is medium, survival low, and the migration high.

If the population is medium and the environment is hostile *then* fecundity and survival are low and the migration high.

If the population is large and the environment is favorable *then* the fecundity is medium, the survival low, and the migration moderate.

If the population is large and the environment is slightly unfavorable *then* the fecundity and the survival are low and the migration high.

If the population is large and the environment is hostile *then* the fecundity and the survival are low and the migration high.

The Mamdani fuzzy inference combines the pertinence degrees associated with each input value by the minimum operator and aggregates the rules through the maximum operator. This method expects the output membership functions to be fuzzy sets and was employed in order to evaluate fuzzy rules and produce output for each rule as follows:

Rule 1: **If** x is A_1 and y is B_1, **then** z is C_1.
Rule 2: **If** x is A_2 and y is B_2, **then** z is C_2.

The method described by Figure 4 has a fuzzy set as output. The process, which converts this set into a numeric value, is known as defuzzification. Specifically, in this study we employed the centre of area method or centre of gravity written as:

$$\bar{z} = \frac{\int_R z.C(z)dz}{\int_R C(z)dz}$$

where R is the bold area at Figure 4. Simulations were run by using equation (3) with each iteration having the parameters F, S, and m estimated with Matlab toolbox Fuzzy, Version 6.0.

RESULTS AND DISCUSSION

Unilateral migration ($m_2 = 0$) in *L. eximia* from a hostile to a slightly unfavorable environment produced local extinction in n_1, and n_2 exhibited a positive monotonic stable equilibrium (Fig. 5A). However, bilateral migration avoided local extinction, leaving
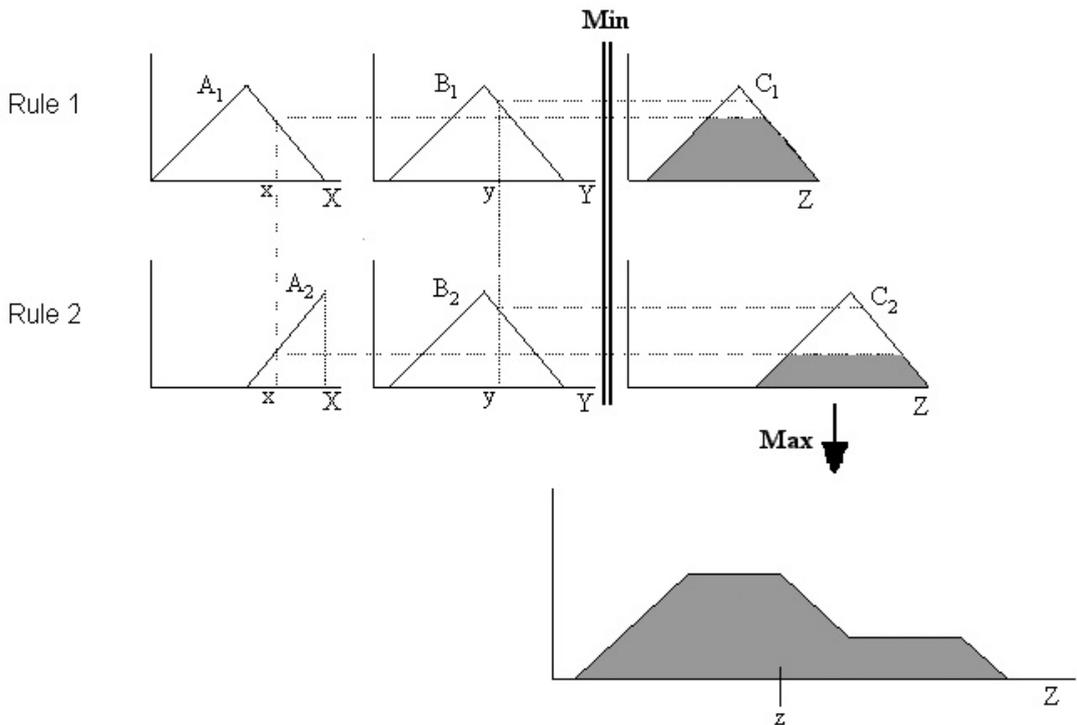
Figure 4: Mandani model with composition Max-min.

the two populations with values above zero (Figs. 5B and D). When comparing figures 5A and 5B, we can see that the bilateral migration avoids local extinction. When comparing figures 5C and 5D, which show unilateral and bilateral migration respectively from a slightly unfavorable to a favorable environment, the positive influence of the bilateral migration on n_1 is evident.

When simulating migration from hostile to slightly unfavorable environments for *C. albiceps,* similar results were observed. With unilateral migration, a local extinction was found, and with bilateral migration, no extinction was observed (Figs. 6 A – D). Specifically, when comparing figures 6C and 6D, it is possible to observe the same result found in figures 5C and 5D. From favorable to slightly unfavorable environments, *C. albiceps* exhibited a stable equilibrium for both coupled populations when the migration was unilateral (Fig. 7A). However, with bilateral migration, both populations exhibited a two-point limit cycle and out-of-phase oscillations (Figs.

7B). Between favorable environments and under unilateral migration, one population exhibited a two-point limit cycle and the other, a monotonic stable equilibrium (Fig. 7C). However, with bilateral migration, both populations exhibited a two-point limit cycle and out-of-phase oscillations.

The main results found in this study were the different dynamic behaviors produced by migration between coupled populations and the rescue effect generated by the connection between them. It is also possible to conclude that environmental heterogeneity can play an important role in blowfly metapopulation systems. Populations produced in different environments in terms of quality may induce distinct results with respect to population dynamics, including out-of-phase oscillations (Fig. 7D), which can increase the chance of local or global persistence (Svensson, 1999; Godoy and Costa, 2005).

On a very interesting note, Rohde and Rohde (2001) investigated how the confusion of subpopulations with metapopulations may affect the

demonstration of complex behavior fluctuations in population size. They showed that fluctuations in population size are very sensitive to the number of subpopulations with different growth rates (i.e., the heterogeneity of the metapopulation) and the initial population size (Rohde and Rohde, 2001). With these results, it is possible to conclude that the lack of unambiguous evidence for chaos in natural populations (Berryman, 1999; Turchin and Ellner, 2000) could be due to the fact that several studies supposedly focusing on subpopulations should be focused on metapopulations (Rohde and Rohde, 2001).

Environmental heterogeneity frequently has been studied in the context of source-sink dynamics (Pulliam, 1988; Pulliam, 1996;

Frouz and Kindlmann, 2001). A source is a subpopulation in which births exceed deaths and emigration exceeds immigration and which may be considered a net exporter of individuals (Pulliam, 1988). A sink, on the other hand, is a subpopulation in which deaths exceed births and immigration exceeds emigration (Pulliam, 1988). In the real world, some habitats are clearly more suitable for survival and/or reproduction than others (Pulliam, 1996). Hence, individuals migrating between habitats of different quality are subjected to life-condition change, which can affect their growth rates (Roughgarden, 1998). Therefore migration and quality of environment are important factors to prevent extinction in sink populations (Pulliam, 1996; Frouz and Kindlmann, 2001).
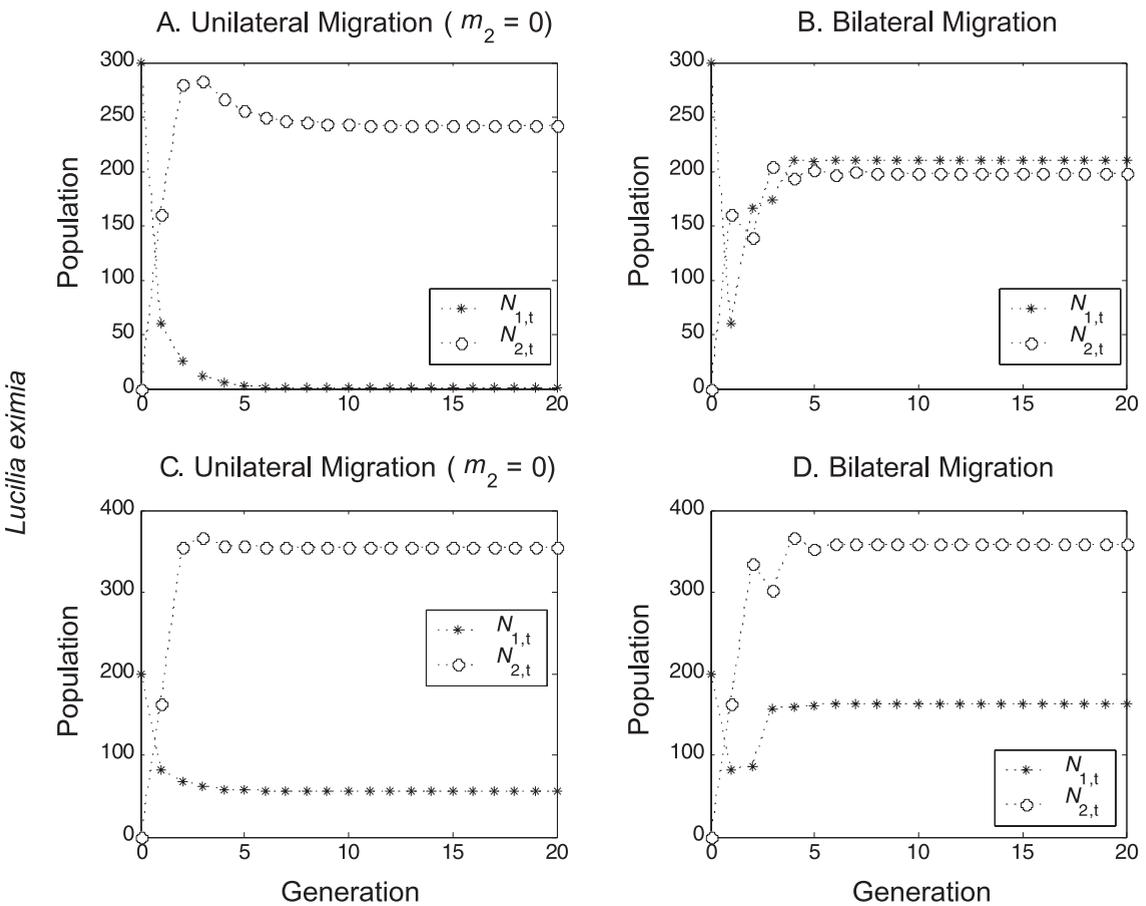

Figure 5: Recursion for twenty generations with $N_{1,0} = 300$ and $N_{2,0} = 0$ simulating unilateral migration (A) and bilateral migration (B) from hostile to slightly hostile environments. Recursion having $N_{1,0} = 200$ and $N_{2,0} = 0$, with unilateral (C) and bilateral (D) migration from slightly unfavorable to favorable environments.
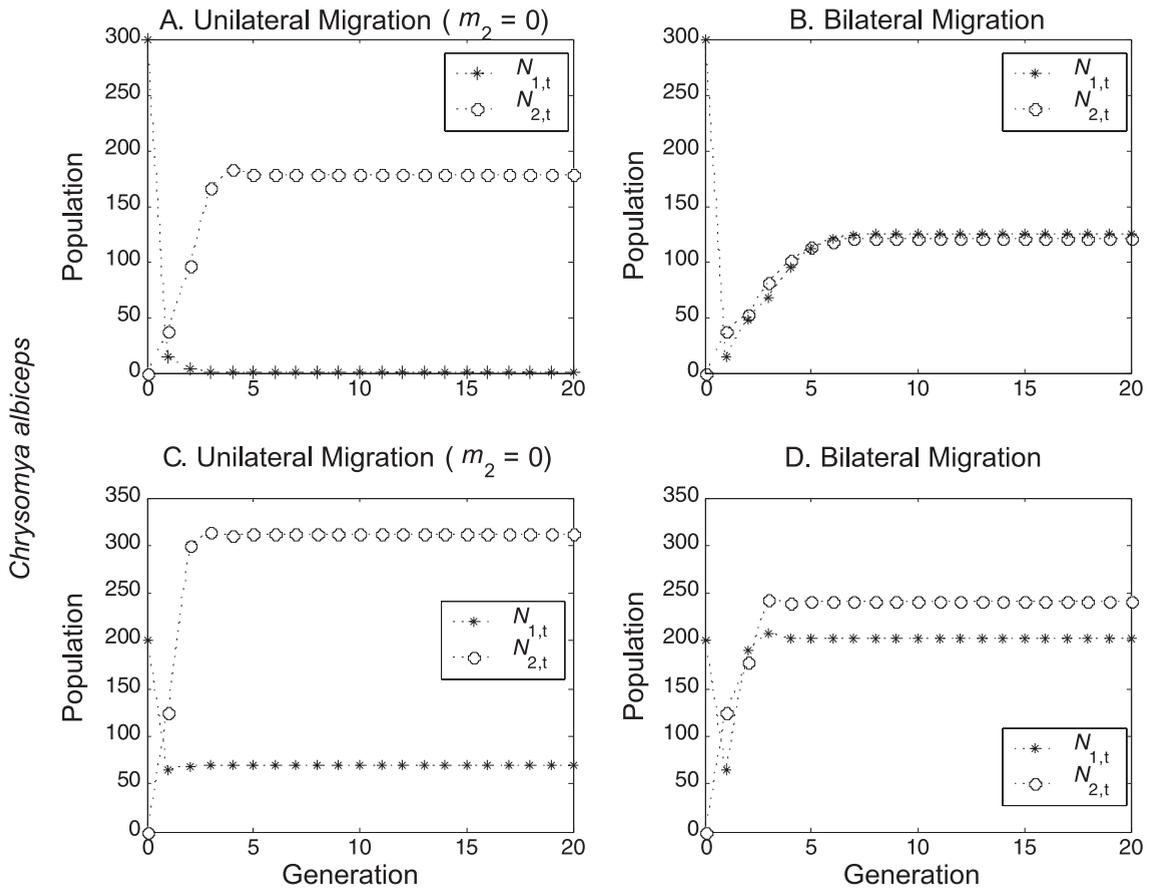
Figure 6: Simulations in populations of *Chrysomya albiceps*. A and B: $N_{1,0} = 300$ and $N_{2,0} = 0$, with migration ($m_2 = 0$) between hostile and slightly unfavorable environments (0.1 in population 1 and 0.4 in population 2) with unilateral migration ($m = 0$) in A and bilateral migration in B. In C and D $N_{1,0} = 200$ and $N_{2,0} = 0$, respectively, migration between slightly unfavorable and favorable environments (0.6 in population 1 and 0.7 in population 2), with unilateral migration for C and bilateral migration for D.

The effect of random environmental variation on population dynamics also has been well documented (Goodman, 1987; Pimm, 1991; Ariño and Pimm, 1995). A population in a variable environment with exchange of individuals between subpopulations will experience variation in both time and space. At any given moment, each subpopulation cannot be correlated perfectly with other subpopulations (Ranta et al., 1995). Hence, both the degree of correlation with environmental variation and the dispersal pattern among subpopulations could affect local and global dynamics. We observed that the environmental heterogeneity was capable of

influencing both the persistence and the population dynamic behavior. However, *C. albiceps* seems to have suffered more influence from migration and quality of the environment than *L. eximia,* since these two factors have produced changes of dynamic behavior in *C. albiceps* but not in *L. eximia.*

In terms of persistence, the two species apparently suffered the same influence from the factors. The good performance of the species analyzed by the theoretical approach can be explained by at least two biological reasons: the pattern of population dynamics and larval behavior. *Lucilia eximia* is a species that exhibits a weak association between seasonal factors and

abundance, since it is found practically every month of the year (Moura et al., 1997; Carvalho et al., 2004). In addition, this species may avoid negative interactions with other species as for example the predator species *C. albiceps* – by visiting carcasses in the initial stages of decomposition, when other blowfly species are not yet present (Moura et al., 1997). *Chrysomya albiceps,* on the other hand, is a larval intraguild predator species and, therefore, can exhibit an alternative way to obtain food resources under food scarcity (Faria et al., 1999; Rosa et al., 2004).

Approaches focusing on metapopulation and environmental heterogeneity have been uncommon in insects, principally studies combining theory and experimentation. Recently, Godoy and Costa (2005) investigated the effect of migration on the length of persistence of coupled local populations of *Tribolium* in different environments to analyze how spreading the risk works. They observed that high environmental heterogeneity was associated with the longest population persistence (Godoy and Costa, 2005). However, no systematic study has been proposed to compare the vulnerability of introduced and native blowfly species to local and global extinction in a metapopulation context, taking account different levels of environmental heterogeneity, as proposed in this study.
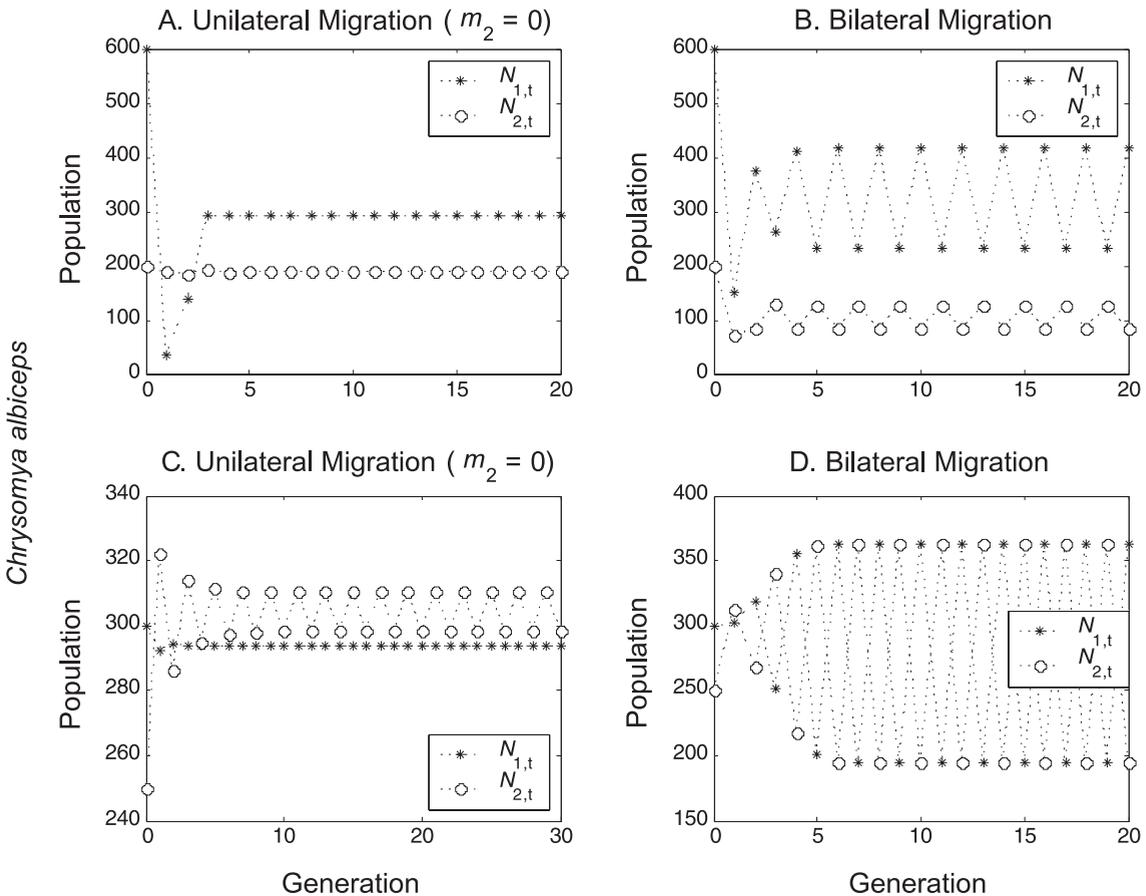

Figure 7: Simulations in populations of *Chrysomya albiceps*. A and B with $N_{1,0}$ = 600 and $N_{2,0}$ = 200 respectively, favorable environmental in population 1 (0.9) and slightly unfavorable in population 2 (0.5), having unilateral migration for A and bilateral migration for B. For C and D $N_{1,0}$ = 300 and $N_{2,0}$ = 250 respectively, with favorable environments (1 for population 1 and 0.95 for population 2), having unilateral migration in C and bilateral migration in D.

We have introduced the idea of using fuzzy logic to investigate the population dynamics of blowflies. Fuzzy logic controllers are commonly used to control systems with complex and unknown dynamics, but for expositional clarity here we have given an example of its use with the well-studied blowfly system (Godoy *et al.,* 2001; Silva *et al.,* 2003).

The fuzzy theory employed here resulted in important findings since, based on scientific intuition, it was possible to incorporate the subjectivity of the biological information into the model. The fuzzification of the parameters of the model allowed fluctuation inherited from the population process (Godoy et al., 2001). New studies employing the fuzzy approach in dynamics of interaction are encouraged in order to contribute for the understanding of the structure of complex systems like the blowfly community.

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