

STASE, METAMORPHOSIS AND COMPETITION IN INSECTS AND OTHER ARTHROPODS

par

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SUMMARY

Based on the stase concept and derived from the Gause model, a new and simple model is proposed to describe the competition between species with complex life cycles (CLCs). Two such species are shown to be able to coexist within the same limited space depending on the population parameters and environment capacity. It is suggested that the metamorphosis and other CLCs would have developed as an inevitable effect of minimizing constraints due to competition and would be a key factor in the diversification of insects and other arthropods.

Keywords : Arthropoda, Insecta, model, instar, CLC (Complex Life Cycle), postembryonic development, diversity

Stase, Métamorphose et Compétition

RÉSUMÉ

Stase, métamorphose et compétition chez les insectes et autres arthropodes. A partir du concept de stase et du modèle de Gause, un nouveau modèle simple est construit pour décrire la compétition entre espèces à cycle vital complexe. Le modèle montre que, en fonction des paramètres démographiques et de la capacité de l'environnement, deux espèces de ce type peuvent coexister dans un même espace limité. Dans une telle approche, l'unité utilisée pour l'analyse des communautés d'arthropodes n'est plus l'espèce, mais la stase. L'hypothèse est avancée, selon laquelle la métamorphose et autres cycles vitaux complexes se seraient développés comme le résultat inévitable de la minimisation de contraintes dues à la compétition et seraient un facteur clé de la diversification des insectes et autres arthropodes.

Where does all this leave the dogma of insect growth by molting? Obviously, it leaves it in something of a shambles. A much better generalization would be insect development « by molting » for that would bring metamorphosis into the picture.

C. M. WILLIAMS (1980 : 382)
Insect Biology in the Future

During 1980s the challenge is to formulate new models that can serve as useful simplifications for community processes in systems to which current theory is largely irrelevant.

J. ROUGHGARDEN (1983 : 598)
Competition and theory in community ecology

All scientific knowledge can be thought as a model of the reality, a model which is continually updated as new information accumulates.

P. A. KEDDY (1989 : 48)
Competition

INTRODUCTION

The phenomenon of metamorphosis in insects -and also in other animals- has stimulated the thinking of biologists since the time of ARISTOTLE. Even poets (for example, GOETHE who wrote a poem on animal metamorphosis) and philosophers (for example, the chapter « Zur Philosophie und Wissenschaft der Natur » in the book « Vereinzelt, jedoch systematisch geordnete Gedanken über vielerlei Gegenstände » written by SCHOPENHAUER in 1851) have speculated on the role and function of metamorphosis. Paradoxically, even if numerous theories and ideas have been proposed to explain what metamorphosis is (e.g. LAMEERE, 1900 ; PÉREZ, 1903 ; BERLESE, 1913 ; POYARKOFF, 1914 ; HENSON, 1946 ; HINTON, 1948 ; SNODGRASS, 1954, etc), it seems that its biological significance is not fully understood. First, metamorphoses must be considered as a special case of a complex life cycle (CLC). As defined by SLADE and WASSERSUG (1975), CLCs occur whenever organisms pass through two or more distinct ecological and morphological phases for each complete generation. Most common hypotheses view metamorphosis and other CLCs either as a mechanism for predator escape (through adult dispersal) or as a mechanism for reducing competition between stages in the life cycle (by evolving distinct ecological stages). SOUTHWOOD (1978) concludes that metamorphosis enables species to avail themselves of a sequence of niches, utilising resources (food, shelter) that may be separated in both time and space and might not, on their own, be adequate for a whole generation or season. More recently, BERNAYS (1986) attributes nutritional advantages to holometabolous development. However, apart from wordy speculations, few models have been proposed to provide alternative hypotheses that can be tested or falsified. ISTOCK (1967) proposed a life table model and concluded that CLCs are inherently unstable over evolutionary time, hence the name of « Istock's dilemma ». Another model was proposed by BRYANT (1969). It is based on habitat selection in a spatially heterogeneous environment and predicts that such a system should favor the evolution of holometabolous development.

Herein a new approach is proposed which relies on two seemingly unrelated observations. First, the number of species in insects and other arthropods seems to be astronomic. As outlined by JANZEN (1977), the number of species of insects is largely a function of how many species can coexist in a habitat. This clearly implies that interspecific competition must be minimized in one way or another if many species are to coexist. Second, insects and other arthropods have a discontinuous development. In primitive forms, the ontogeny is a succession of stages which are more or less similar and their ontogenetic trajectory, *sensu* ANDRÉ (1988), looks like a short, straight line. In most evolved groups, as the ontogeny becomes a complex life cycle, the ontogenetic trajectory is represented by a zig-zag line, more or less lengthened. Therefore, it was tempting to relate the CLC development of insects to their high diversity and the subsequent minimization of interspecific competition.

To set up the new model, two basic approaches have been called forth. The first is the stase concept, which has been used to take account of the discontinuous ontogeny observed in mites and other arthropods. The second will formalize the interspecific competition and is essentially the classical Gause model.

TWO BASIC APPROACHES

The stase concept

As early as 1873, Sir JOHN LUBBOCK drew a fundamental distinction between animals with different terminal or mature forms and animals which pass through a succession of different forms in the course of their development. He proposed to restrict the term polymorphism to the occurrence of different terminal or mature forms and to call polyeidism the succession of different forms in the course of development. As noticed by WIGGLESWORTH (1954), the essential feature of polymorphism is multiple potentiality, but only one form is realized, all the others remaining latent or suppressed. Conversely, multiple potentiality expressed through polyeidism results in the coexistence of different forms in the same individual, these forms succeeding one another during the course of its ontogeny.

These successive morphs succeeding one another during development conform with the concept of stase propounded by the French acarologist, F. GRANDJEAN (1938, 1951, 1957, 1970). A stase is defined as one of the successive forms through which an arthropod passes, these forms being fundamentally different from one another by the criterion of « all or none ». The criterion of « all or none » means that an organ exists in one form but is absent in another. As emphasized in a previous publication (ANDRÉ, 1988, 1989), the stase concept differs in basic ways from those used in the instar-stage-stadium terminology (Table 1).

In actinotrichid mites and in some insect groups (*e.g.* in Thysanoptera), the difference between stase and instar may appear to be subtle since the number of instars is fixed and corresponds to the number of stases. In some other arthropods however, the number of instars is undefined and variable while the number of stases is well-defined and fixed. This is the case in Collembola where the number of stases

is either six or seven depending on the species (ANDRÉ, 1986, 1987) and in Lepidoptera where the number of larval instars may be highly variable although there are only two larval stases (ANDRÉ, 1989).

TABLE 1
Major features discriminating stases from instars
(From ANDRÉ, 1989)

INSTAR	STASE
Defined by reference to molts Two successive instars may be quite similar Allometric characters suffice to discriminate instars Often related to growth Not necessarily homologous from one species to another Number constant or variable If variable, number environmentally determined	No explicit reference to molts (3) Any stase is characterized by all or none criteria applied to idionymic characters (1, 2, 3) Only meristic characters may discriminate stases (1, 2) Related to development ; a stase is a level of development (2, 3) Stases of different species may be idionymic (homologous) (2, 4) Number constant (?) Number genetically fixed

(1) GRANDJEAN (1938) — (2) GRANDJEAN (1957) — (3) GRANDJEAN (1970) — (4) HAMMEN (1966, 1978).

The Gause model

The Gause model (GAUSE, 1935) is based on a simple logistic equation :

$$dN/dt = r \cdot N \cdot (K - N)/K \quad (1)$$

where N represents the number of individuals,

r is the intrinsic rate of increase of the species,

K is the carrying capacity of the environment, i. e. the maximum population size possible.

The equilibrium density, N^* , is observed when the species reaches the carrying capacity, i.e.

$$N^* = K \quad (2)$$

In the Gause model, also known as the Lotka-Volterra equations, the growth of two species, forced to compete in a limited amount of space and each with a definite K level, is represented by a pair of differential equations similar to (1) :

$$dN_A/dt = r_A \cdot N_A \cdot (K_A - N_A - \beta N_B)/K_A \quad (3)$$

$$dN_B/dt = r_B \cdot N_B \cdot (K_B - N_B - \alpha N_A)/K_B \quad (4)$$

where α and β are the competition coefficients of species A and B , respectively, and represent the inhibitory effect of one species on the other.

The four possible outcomes of competition for such species that are forced to compete in a restricted space are well-known and can be determined graphically as shown in Fig. 2. The major conclusion to be drawn is that, except in a special case (case (4) in Fig. 2), only one of the two species will survive.

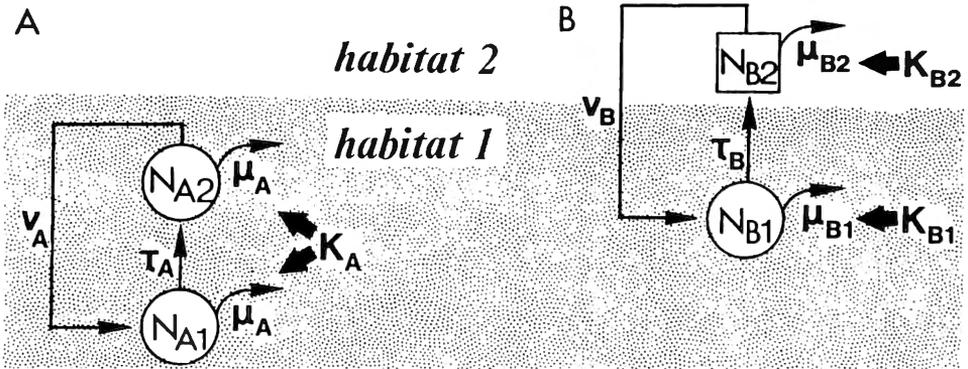


Fig. 1. — Life cycles of one species with two instars (A) and another with two stases (B). Symbols are : N : number of individuals, v : birth rate, τ : transformation rate, μ : mortality rate, K : carrying capacity of the environment. The first subscript refers to the species (A or B), the second designates the level through ontogeny (1 or 2).

SINGLE SPECIES MODELS

This section is aimed at formalizing the concept of stage in contrast to that of instar and integrating stages into a population dynamics perspective. Practically speaking, the problem consists of determining how these concepts may be conveniently embodied in equations.

Species with instars

Let us suppose a species with merely two instars, or possibly two homeomorphic (similar) stases, as in Fig. 1A. All characteristics of both instars are thus identical except that instar 2 (adult) reproduces while instar 1 does not. Growth equations for a species living alone are then, using the symbols in Fig. 1A,

$$dN_{A1}/dt = (v_A N_{A2} - \tau_A N_{A1} - \mu_A N_{A1}) \cdot Z_A \quad (5)$$

$$dN_{A2}/dt = (\tau_A N_{A1} - \mu_A N_{A2}) \cdot Z_A \quad (6)$$

which when added give

$$dN_A/dt = (v_A N_{A2} - \mu_A N_A) \cdot Z_A \quad (7)$$

where

$$N_A = N_{A1} + N_{A2} \quad (8)$$

and

$$Z_A = (K_A - N_A) / K_A \quad (9)$$

Z_A thus represents the receptivity of environment to species A . Z_A is maximum in the absence of species A and tends to zero when the density of species A approaches the carrying capacity of the environment.

The equilibrium density, N^* , of such a species is reached at the saturation level of the environment, i.e. when

$$N^*_A = K_A \quad (10)$$

Species with stases

Let us suppose a species having a CLC with heteromorphic (distinct) stases as species B in Fig. 1B. The two stases are supposed to occupy different ecological niches. For instance, larvae may be active wrigglers in the water whereas adults are flying and live far away from water. As stases are distinct, different values are attributed to mortality rates and environmental saturation levels depending on the stases. Growth equations of such a species are (symbols as in Fig. 1B) :

$$dN_{B1}/dt = (v_B N_{B2} - \tau_B N_{B1} - \mu_{B1} N_{B1}) \cdot Z_{B1} \quad (11)$$

$$dN_{B2}/dt = (\tau_B N_{B1} - \mu_{B2} N_{B2}) \cdot Z_{B2} \quad (12)$$

where

$$Z_{B1} = (K_{B1} - N_{B1})/K_{B1} \quad (13)$$

$$Z_{B2} = (K_{B2} - N_{B2})/K_{B2} \quad (14)$$

Equations (11), (12) and (13) are isomorphic to equations (5), (6) and (9), respectively.

The maximum density reached by each stase depends on the ratios between the values of carrying capacities compared to the ratio of the birth and transformation rates. If

$$v_B/\tau_B > K_{B2}/K_{B1} \quad (15)$$

then, the adult environment is saturated first (see Table 2). At saturation of the adult environment, equations (12) and (11) become, respectively :

$$dN_{B2}/dt = 0 \quad (16)$$

$$dN_{B1}/dt = (v_B K_{B2} - \tau_B N_{B1} - \mu_{B1} N_{B1}) \cdot Z_{B1} \quad (17)$$

where the product $(v_B K_{B2})$ is constant whereas N_{B1} may still increase. Equation (17) will be equal to zero when

$$N_{B1} = K_{B2} \cdot v_B / (\tau_B + \mu_{B1}) = Max_{B1} \tag{18}$$

The value reached by N_{B1} in equation (18) represents the maximum larval density, Max_{B1} , determined from population parameters. If Max_{B1} is smaller than K_{B1} , i.e. if the larval density allowed by population parameters, does not reach the environment saturation level, then the larval habitat will remain unsaturated. Otherwise, the larvae will grow until the habitat is saturated.

The same reasoning applies when

$$v_B / \tau_B < K_{B2} / K_{B1} \tag{19}$$

i.e. when the larval environment is saturated first. At saturation of the larval habitat, equations (11) and (12) can be rewritten as :

$$dN_{B1} / dt = 0 \tag{20}$$

$$dN_{B2} / dt = (\tau_B K_{B1} - \mu_{B2} N_{B2}) \cdot Z_{B2} \tag{21}$$

The maximum adult density, Max_{B2} , determined from equations (20) and (21) will be :

$$Max_{B2} = K_{B1} \cdot \tau_B / \mu_{B2} \tag{22}$$

Depending on whether Max_{B2} is greater or smaller than K_{B2} , the adults will or will not reach the saturation threshold of their environment.

TABLE 2

The saturation of environments by a species with two stases

IF		HABITAT OF	
		LARVAE	ADULTS
$v_B / \tau_B > K_{B2} / K_{B1}$	$Max_{B1} > K_{B1}$	unsaturated	saturated
	$Max_{B1} < K_{B1}$	saturated	saturated
$v_B / \tau_B = K_{B2} / K_{B1}$		saturated	saturated
$v_B / \tau_B < K_{B2} / K_{B1}$	$Max_{B2} > K_{B2}$	saturated	saturated
	$Max_{B2} < K_{B2}$	saturated	unsaturated

$$Max_{B1} = K_{B2} \cdot v_B / (\tau_B + \mu_{B1}) \quad Max_{B2} = K_{B1} \cdot \tau_B / \mu_{B2}$$

The possible outcomes are summarized in Table 2. It turns out that the outcomes do not depend on the initial densities, but only on the environment capacity and population parameters. For instance, if the larval environment is saturated first, the transformation rate is a key factor regulating the saturation or non-saturation of the adult environment while the birth rate has no effect on the outcome.

Conversely, if the adult habitat is saturated first, the birth rate is an important parameter in determining the saturation or non-saturation of the larval environment.

A major consequence of the occurrence of stases in arthropod ontogeny is that the successive habitats colonized by a species are not necessarily saturated, which means that there is some room available for another species to coexist, as demonstrated in the next section.

TWO SPECIES MODELS

From the basic model described in the previous section are derived models where two species are implicated. Four sets of simulations corresponding to different situations will be analyzed. In the simplest case, two species with mere instars will be forced to compete. In the next set of simulations, one of the species will have a CLC with two stases. The last two sets will treat systems with two species, both of which have two stases.

Two species with instars

In this first set of simulations, the two species have merely two instars as in Fig. 1A. All characteristics of both instars are thus identical except that one reproduces and the other does not (see previous section). If two such species are forced to coexist in a limited space, simultaneous growth equations are :

$$dN_A/dt = (v_A N_{A2} - \mu_A N_A) \cdot Z_A \quad (23)$$

$$dN_B/dt = (v_B N_{B2} - \mu_B N_B) \cdot Z_B \quad (24)$$

Equations (23) and (24) are similar to equation (7) except that the environmental receptivity, Z , takes into account the interspecific competition :

$$Z_A = (K_A - N_A - \beta N_B) / K_A \quad (25)$$

$$Z_B = (K_B - N_B - \alpha N_A) / K_B \quad (26)$$

where α and β are competition coefficients of species A and B respectively.

The four possible outcomes of the competition between the two species are identical with those predicted by the classical Gause model. The corresponding zero growth isoclines are given in Fig. 2. It must be emphasized that the outcome is again independent of the initial densities, except for case (4).

This first set of simulations is essential. Indeed, it clearly shows that species having mere instars do not differ in their population dynamics from others having a continuous development. The fact of dividing the ontogeny into a succession of instars, i.e. discrete units having similar ecological requirements, does not change anything in the conclusions of the classical Gause model. Provided that the population parameters (natality, mortality rates, etc.) are the same, the behavior of species

(i.e. their variation in density) and the outcome of competition are identical for species with a continuous development or with an ontogeny composed of instars.

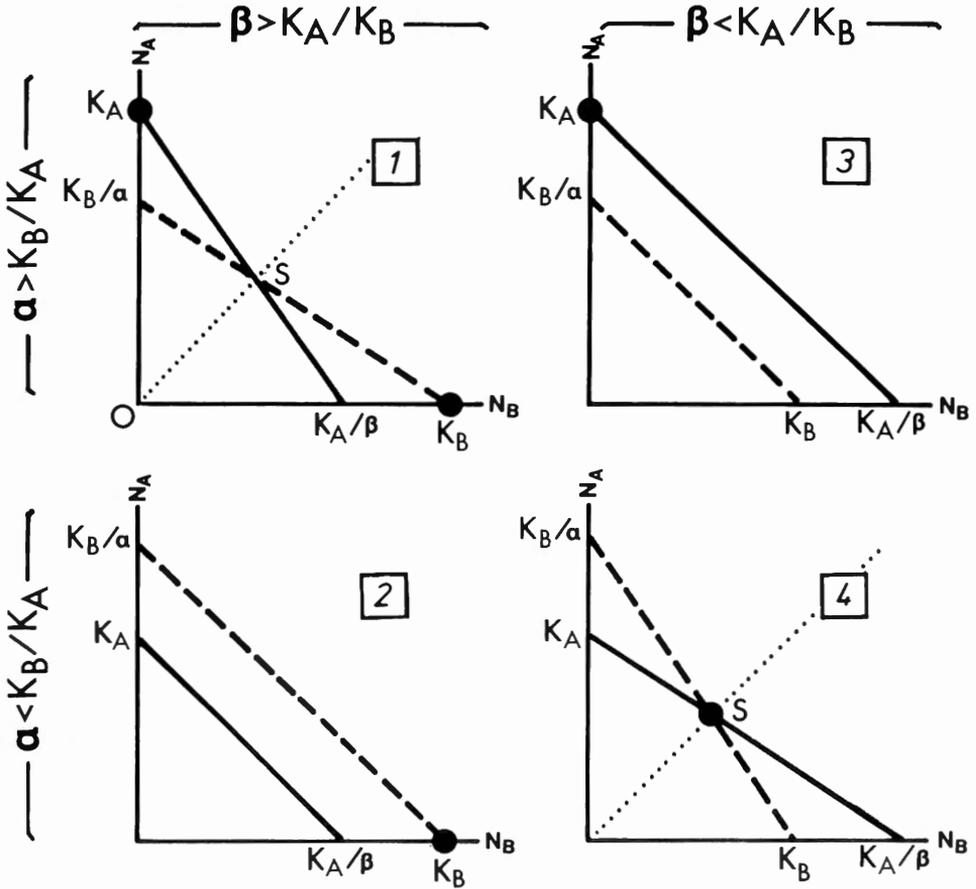


Fig. 2. — Competitive interactions between two species with instars. The four cases and the corresponding conditions are the same as in the Gause model. The solid line represents the zero growth isocline of species *A* while the dashed line refers to species *B*. Black circles represent stable equilibrium points.

One species with instars, another with stases

In this set of simulations, species *A* is supposed to have instars while species *B* develops through two stases. This situation corresponds to Figure 1.

If the maximum density of species *B* larvae, Max_{B1} (see eq. 18), is equal to or greater than the saturation level, K_{B1} , then the outcome is of course similar to that predicted by the classical Gause model. If not, the outcome may be determined by zero growth isoclines as in Fig. 3.

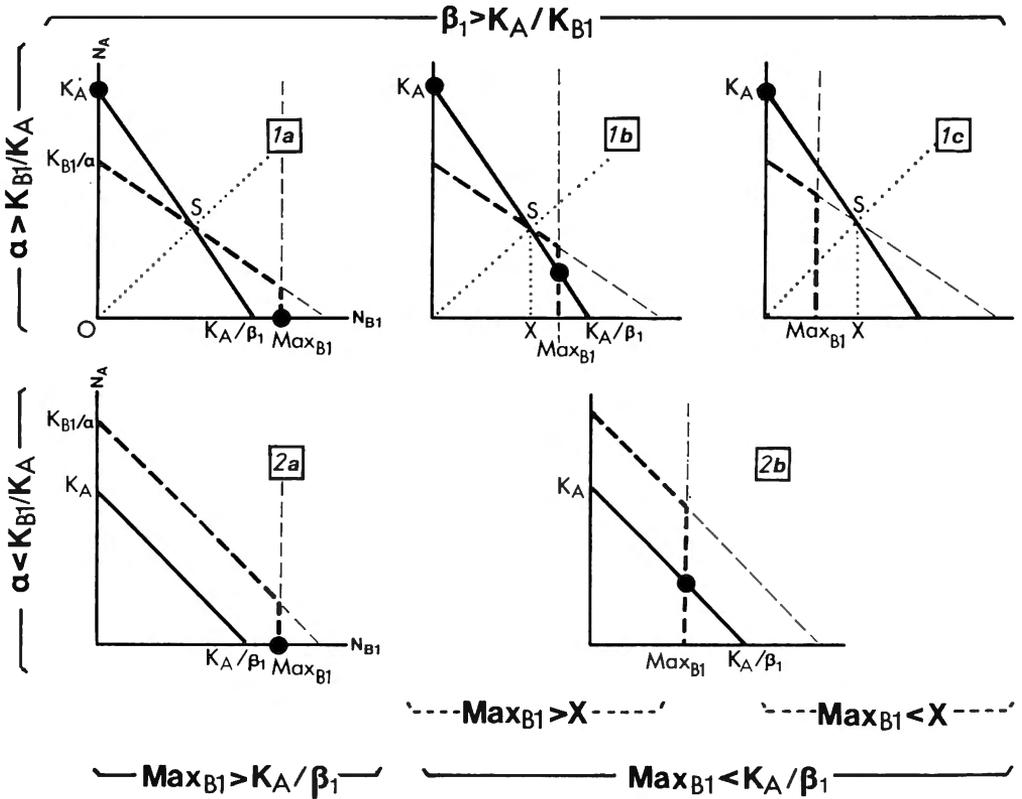


Figure 3 is similar to the zero growth isoclines determined by the Gause model, except that a third isocline, corresponding to Max_{B1} , intercepts the two others. Case (1) of the Gause model (Fig. 2) must be decomposed into three subcases depending on the value of Max_{B1} . If Max_{B1} is greater than K_A/β_1 , only one species survives and the outcome depends on the initial densities exactly as in the Gause model. If Max_{B1} is smaller than K_A/β_1 but greater than X (X corresponds to the abscissa of the crossing point S), then an equilibrium is possible depending on the initial densities (case (1b) in Fig. 3). In the triangle $S - K_A - K_{B1}/\alpha$, species B larvae are above their saturation level while species A is not; thus if a mixture composed of larvae B and species A is represented by a point located in that triangle, larvae of species B will diminish while species A will continue to increase until species A survives alone. Similarly, if a mixture of larvae B and species A is represented by a point located in the triangle $S - K_{B1} - K_A/\beta$, then larvae of species B should continue to increase while species A should vanish. However, the increase of larvae B is limited by the third isocline, the vertical line corresponding to Max_{B1} in Fig. 3. As a result, the growth of larvae B will stop or be brought back at that value and a equilibrium point is determined by the crossing of the vertical isocline and zero growth isocline of species A . The values of that point are :

$$N^*B_1 = Max_{B1} = K_{B2} \cdot v_B / (\tau_B + \mu_{B1}) \tag{27}$$

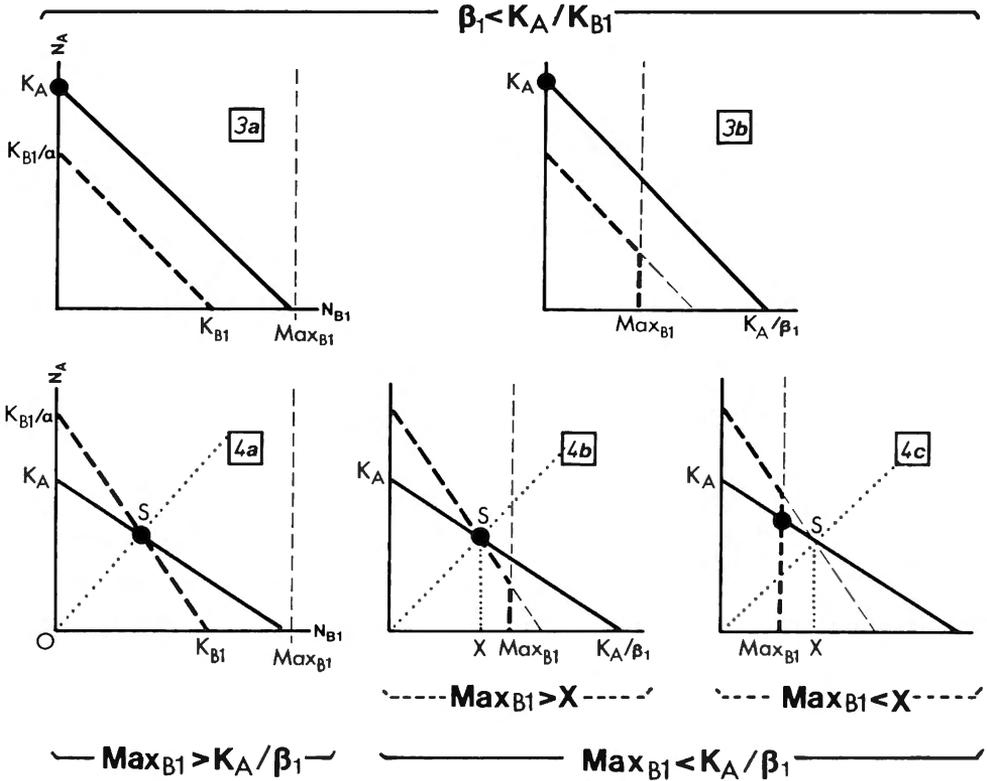


Fig. 3. — Competitive interactions between two species, one with two instars (*A*) and the other with two stases (*B*). Only larvae of species *B* are competing with all individuals of species *A*. The four major cases (1 to 4) answer the same conditions as those defined in Fig. 2. The solid line represents the zero growth isocline of species *A* while dashed line refer to species *B* larvae.

$$N^*_A = K_A - \beta \cdot Max_{B1} \tag{28}$$

while N^*_{B2} will be equal to K_{B2} .

Lastly, if Max_{B1} is smaller than X , then species *A* will always be the sole survivor (case 1(c) in Fig. 3).

Case (2) of the Gause model must be decomposed into two subcases, again depending on the value of Max_{B1} . If Max_{B1} is greater than or equal to K_A/β_1 , then species *B* will always survive whatever the initial densities (case 2(a) in Fig. 3). But if Max_{B1} is smaller than K_A/β_1 , then an equilibrium will be reached (case 2(b) in Fig. 3).

Similarly to case (2), case (3) of the Gause model may be subdivided into two subcases depending on the value of Max_{B1} . In both subcases (3a and 3b in Fig. 3), only species *A* will survive.

Lastly similarly to case (1), case (4) of the Gause model may be subdivided into three subcases (cases (4a), (4b) and (4c) in fig. 3). In all subcases, an equilibrium is observed. Note that in case (4c), the equilibrium point does not correspond to the crossing point S contrary to the two other subcases.

In conclusion, there are ten subcases distinguished in Fig. 3. In four subcases, an equilibrium will always be reached while, in one subcase (2b), an equilibrium may be observed depending on the initial densities (Table 3).

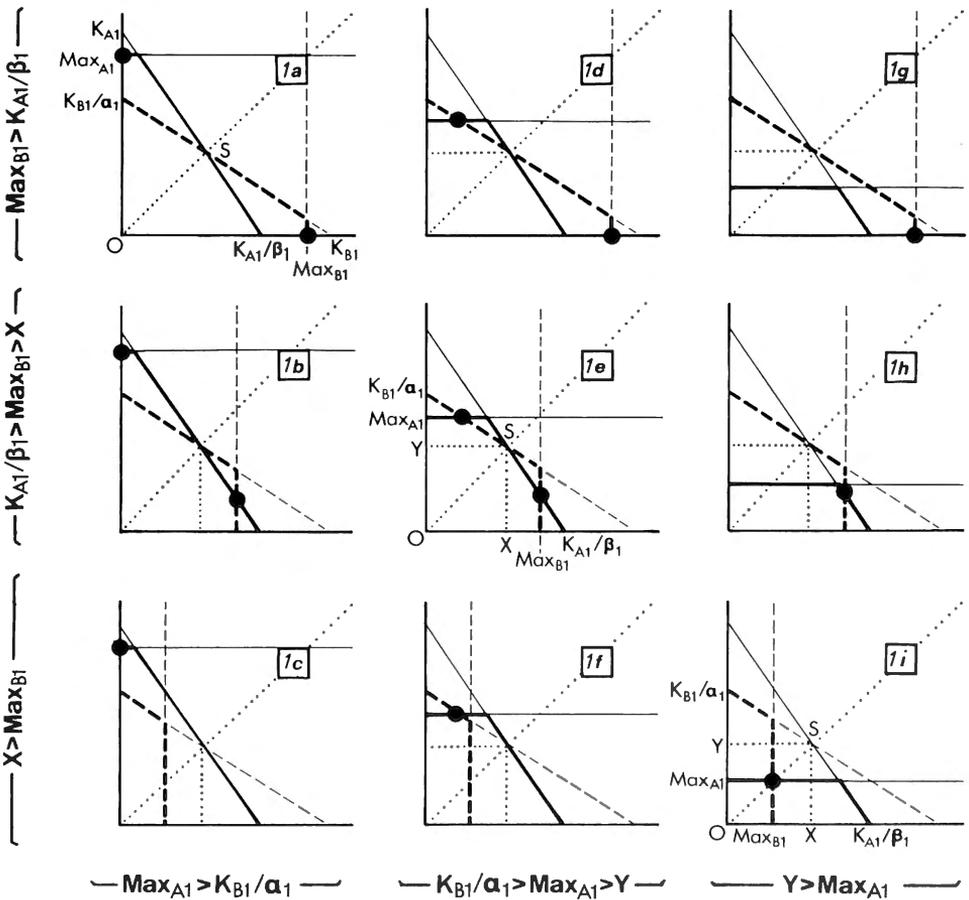


Fig. 4. — Competitive interactions between larvae of two species with stases when $\alpha_1 > K_{B1}/K_{A1}$ and $\beta_1 > K_{A1}/K_{B1}$ (case 1 in Fig. 2). Nine subcases are distinguished depending on the values of Max_{A1} and Max_{B1} . Solid lines represent the zero growth isoclines of species A larvae while dashed line refer to species B larvae.

Two species with stases (one-level competition)

In this situation, both species are supposed to have stases as in Fig. 1B but the competition is restricted to one stage, for instance to larvae. In parallel to the previous section where case (1) of the Gause model was subdivided into three subcases depending on the value of Max_{B1} , case (1) must be decomposed into nine subcases depending on the values of Max_{B1} and Max_{A1} (Fig. 4). It is easy to see that an equilibrium point is always reached in four subcases (1e, 1f, 1h and 1i), that it may be observed in two subcases (1b and 1d) depending on the initial densities, and that only one species will always survive in the last three subcases (1a, 1c and 1g).

TABLE 3

Number of possible outcomes in the three situations reported in the text. Max_{B1} is supposed to be smaller than K_A/β_1 . The same assumption applies to Max_{A1} in the third situation. Unstable equilibria are not considered.

Situation	Total number of cases	Number of cases where equilibrium is		
		always reached	possible (1)	never observed
Two species with two instars	4	1	0	3
One species with instars, the other with stases	10	4	1	5
Two species with two stases	26	17	2	7

(1) Depending on initial densities.

Similarly, case (2) of the Gause model must be decomposed into four subcases depending on whether Max_{A1} and Max_{B1} are greater or smaller than K_{A1}/β_1 and K_{B1}/α_1 , respectively. An equilibrium point will be observed if Max_{B1} is smaller than K_{B1}/α_1 whatever the value of Max_{A1} , otherwise only species B will survive. Case (3) is symmetrical to case (2) and an equilibrium point will be reached in two subcases out of four. Lastly nine subcases may be distinguished in case (4) as in case (1); in all nine subcases, an equilibrium is observed.

It turns out that, among the 26 subcases, an equilibrium is always observed in 17 subcases, i.e. in 65 % of the subcases. Table 3 clearly shows that the more complex are the ontogenies, the more probable will be the equilibrium between the two competing species.

Two species with stases (two-level competition)

In all previous sections, the two species were competing with each other at only one level of their ontogeny, for instance at the larval stage. What happens if both

adults and larvae of the two species are competing? Due to space limitation, it is not possible to detail all the possible combinations of such a competition. However, it must be stressed that an equilibrium may be reached even if adults and larvae are both competing. An example of simulation is presented in Fig. 5. In this simulation, species *A* is superior in competitive fitness to species *B* at the larval stage but inferior to it at the adult stage. This simulation is important as it corresponds to experimental data presented by AYALA (1969).

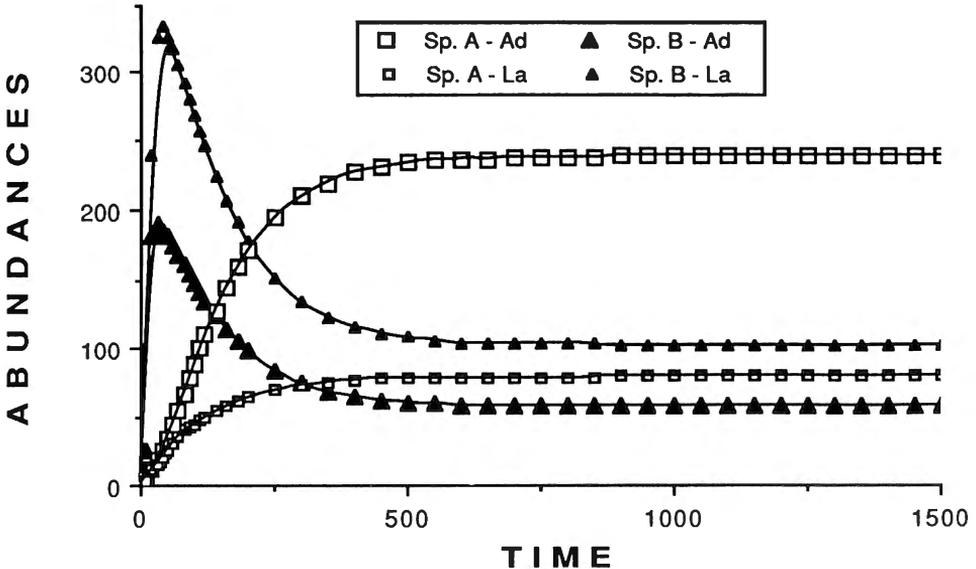


Fig. 5. — Simulation of the growth of two species competing at two levels (larval and adult). Parameters for species *A* are : $v = 0.5$; $\tau = 0.3$; $\mu_1 = \mu_2 = 0.10$; $K_1 = 100$; $K_2 = 500$; $\alpha_1 = 2.5$; $\alpha_2 = 0.6$; for species *B* : $v = 0.9$; $\tau = 0.45$; $\mu_1 = \mu_2 = 0.05$; $K_1 = 500$; $K_2 = 200$; $\beta_1 = 0.2$; $\beta_2 = 2.0$.

DISCUSSION

The stase concept was proposed more than fifty years ago by GRANDJEAN (1938). Although the concept may apply to all arthropods, its use has been confined almost exclusively to mites and its application seems to have been limited to morphology and related evolutionary problems (cf the recent syntheses by ANDRÉ, 1988, 1989). Beyond these limits, the concept might apply equally well to many other domains such as ecology, genetics, and pest control. This paper aims at proposing, for the first time, an hypothesis explaining the existence of stases and the derived phenomena of metamorphosis and CLCs. Specifically, the question of a possible relationship between the discontinuous development of insects and other arthropods and the high species diversity observed in these groups is addressed and explored through a new and simple model derived from the classical Gause model.

The choice of the model

MAY (1973) made a fundamental distinction between « tactical » models which strive for a detailed and pragmatic description of quite specific systems, and « strategic » models which sacrifices precision in an effort to grasp general principles. As emphasized by MAY (1973), strategic models do not correspond in detail to any single real situation but aim to provide a conceptual framework for the discussion of broad classes of phenomena. On the other hand, LEVINS (1968), and later MAYNARD-SMITH (1974), pointed out that we should not look for assertions that are true of all systems. Instead we should look for the causes of differences of behavior between different systems. To answer this type of question, we need models that are as simple as possible (MAYNARD-SMITH, 1974). In other words, the important question is this : does a slightly more complicated model yield significantly more accurate results (GILPIN and AYALA, 1973) ?

Practically speaking, it seems obvious that the new model had to be an extension of the classical Gause model. This model is so popular in ecology that the study of equations themselves is recognized as ecological research (FAGERSTRÖM, 1987). It is the archetype of exploratory models, i.e. models which allow the logical consequences of changes in assumptions or initial conditions to be explored systematically (KEDDY, 1989). In this way, it is possible to meet the first three criteria proposed by GILPIN and AYALA (1973) to arrive at what they call the best model of growth and competition, namely simplicity, reality and generality.

A classical argument advanced against the Gause model is that it is simplistic. Such an argument holds also for the new model. For instance, it assumes that the environment is uniform, which is hardly realistic. It is also simplistic to assume that the environment does not vary in time and there is no delay in the response of each species to the other. It does not account for indirect effects of n -species competition, which can make it extremely difficult to extrapolate results from pair-wise experiments to multi-species interactions (MOEN, 1989). Lastly, the new model is simplistic in that it entails only two stases per species while the ontogeny of insects and other arthropods is generally composed of five or more stases. Nevertheless, all of these assumptions have been retained because the more complex a mathematical model becomes, the less generalized is its applicability to ecological situations. Furthermore, in spite of such simplistic assumptions, this study reveals that the coexistence between species forced to live together in a limited space, at least temporarily, is possible provided that their ontogenies comprise distinct stases.

Other weaknesses of the model are that all the immediate and indirect effects of larval competition are not detailed as in studies propounded by NISBET and GURNEY (1984). The adaptive interactions between successive stases of the same species also are disregarded although it is well known that environmental conditions experienced by larvae can affect the adult population (*see e.g.* SIGURJØNSDØTTIR, 1984 ; PROUT and MCCHESEY, 1985 ; SIMMONS, 1987). However such weaknesses are thought to be inherent to any strategic model; they do not diminish the value of the conclusions drawn from the comparison between the Gause model and the new model derived from it.

Relationships with other models

Comparison with the Gause model

The new differs in basic ways from the Gause model due to the introduction of the stase concept. However, when the differences between stases are reduced to zero, the new model behaves exactly as the Gause model (see the first set of simulation). The latter turns out to be a special case of the former.

There is a second difference. As pointed out by WIENS (1977), in virtually all mathematical treatments of competition, the populations occupying a given environment are supposed to be at their respective carrying capacities, and suitable habitats are thus saturated. WIENS (1977) violently denounces this « assumption which lies at the heart of the classical Lotka-Volterra competition formulation and its extensions ». Obviously, the new model, though derived from the Gause model, escapes this critique.

Age-structure models vs. stase-structure models

Many models of age-structured populations have been proposed (see the synthesis by CHARLESWORTH, 1980). However, it must be emphasized that such models have been designed to apply to both animals and plants with continuous development, as well as to organisms with discrete age classes. It is not by chance that CHARLESWORTH (1980) cited man as one of the two best-known examples of age-structured population.

LEFKOVITCH (1965) was particularly concerned with the population dynamics of insect pests in stored products and noticed that, if it was difficult to estimate the age of these insects, their *stage* could be recognized easily. Accordingly, he proposed, for the first time, a model based on stage groupings rather than age groupings, taking into account the fact that the various stages might have different durations. Despite the numerous models of age-structured populations published subsequent to that of LEFKOVITCH, it was necessary to wait nearly 20 years for the resurrection of the expression « stage structure model » (NISBET and GURNEY, 1984). Nevertheless, the basic assumption underlying most single-species age-structure models still remains that a species has age-specific properties. Even the most recent models applied to insect populations (*e.g.* MACK *et al.*, 1987; CROWLEY *et al.*, 1987) are based on arbitrary age classes which have nothing to do with the stase concept, or even with the instar definition. A remarkable exception must, however, be cited: the application and extension of the Leslie matrix model by HADJIBIROS (1975) and CANCELA DA FONSECA and HADJIBIROS (1977) to an oribatid mite population with five active stases.

Age-structure models and competition

PENNYCUICK *et al.* (1968) first designed an age-structure competition model derived from the Leslie matrix model. Their simulations showed that the outcome of competition depended on the values of the competition coefficients, and possibly on the initial density values. In all cases, however, the outcomes were similar to

those predicted by the corresponding Lotka-Volterra equations, even if a time lag was introduced into the system to determine fecundity.

HASSEL and COMINS (1976) explored the general properties of a single age-class model for two-species competition and concluded that it resembled the Lotka-Volterra model in its general properties, i.e. the zero-growth isoclines were linear and the conditions for coexistence of the two competing species were similar. From this basic model, they derived a two age-class competition model. The introduction of such a minimal age-class structure had interesting consequences as it affected both the shape of the zero-growth isoclines, and the number of possible equilibrium points. The Hassel and Comins' model is however fundamentally different from the model presented herein in that it assumes that the generations and stages are discrete and non-overlapping so that adults and larvae are not present at the same time. Another basic difference is the shape of the zero-growth isoclines which are nonlinear in the Hassel and Comins' model and linear in the new model.

More recently, BELLOWS and HASSEL (1984) developed three models for inter-specific competition in laboratory populations of two species of bruchid beetles. The first two, the single age-class and the two age-class models, predicted an unstable equilibrium, departures from which could lead to the extinction of either species. The third model, derived from a single-species system model previously described by BELLOWS (1982), predicted the inevitable extinction of the species with the longer generation time. The outcomes of the three models are thus fundamentally different from the predictions obtained with the new model proposed herein.

In conclusion, it seems that the introduction of an age-structure into a model for two-species competition does not fundamentally modify the predictions of the basic model. This is in accordance with the results of my competition model where the two species have instars : the predictions of the Gause model still hold.

Comparison with Istock's model

The new model is fundamentally different from ISTOCK's (1967) model, which was based on a life table approach. If Istock's model predicts that CLCs are inherently unstable over evolutionary time, the new model suggests that species occupying the same environments may coexist when their ontogeny comprises distinct stases. The coexistence is possible even if all distinct stases compete at several levels of ontogeny, provided that the successive stases occupy different ontogenetic niches. This recalls, in some respects, the conclusions of BRYANT (1969) that habitat selection in a spatially heterogeneous environment should favor the evolution of holometabolous development.

Field experiments

Among the 164 field experiments on interspecific competition listed by SCHOENER (1983), only 31 (19 %) bear on arthropods (insects : 21, crustaceans : 5, arachnids : 6). Six additional papers deal with arthropods in competition with other taxa. This survey shows that arthropods are dramatically under-represented ; as

pointed out by KEDDY (1989), there is no correspondence between the abundance of organisms in the biosphere and the effort invested in studying them. Similar conclusions may be drawn from the survey undertaken by CONNELL (1983) : out of 72 studies on interspecific competition, only 13 (18 %) are concerned with arthropods.

All the experiments listed in these surveys offer the same bias. Either the arthropod species are treated as a homogeneous entity (i.e. all stases are confused or supposed to be equally competitive) or the experiments focus on only one stase without any reference to the others. The same bias is observed in more recent publications.

To explain the species coexistence observed in many cases, authors invoke either the abundance of food resources (TOKESCHI, 1986), or the absence of strong competitive interactions (GIBSON and VISSER, 1982; STRONG, 1982; TOKESCHI and TOWNSEND, 1987; HUNTER and YEARGAN, 1989), or the spatial aggregation (ATKINSON and SHORROCKS, 1984; ATKINSON, 1985; TOKESCHI and TOWNSEND, 1987). In no case has the existence of successive stases, each with different competitive abilities, been proposed as an explanation to coexistence. However, a recent paper (HOVENKAMP, 1989) is very stimulating, for it shows that the coexistence between *Daphnia* species might be explained in terms of instar-dependent mortality rates.

Other experimental evidences

There is considerable experimental evidence to support the conclusions drawn from the new model. In experiments carried out by PARK (1948) on *Tribolium*, the coexistence of two species was obtained when the system was « open », i.e. when individuals of each species were artificially removed. Similar results were obtained with hydras by SLOBODKIN (1961). The transformation of individuals from one stase to another (see the transformation rate in Fig. 1B) obviously plays the same role as the artificial removal performed by PARK and by SLOBODKIN. This transformation through development also recalls the effect of predation which prevent prey species from competing themselves by depressing their populations (cf. WIENS, 1977).

Another famous experiment carried out by AYALA (1969), who succeeded in rearing *Drosophila serrata* and *D. pseudoobscura* together, also supports the new model. AYALA (1969) explained that *D. serrata* was superior in competitive fitness to *D. pseudoobscura* at the larval stage but inferior to it at the adult stage. This explanation fits the case simulated in Fig. 5. After Ayala's demonstration, GAUSE (1970) correctly argued that his experimental environment contained two habitats : a solid phase and an aerial phase. In reply to GAUSE, AYALA (1970) rightly retorted that the *Drosophila* had to compete in both phases. These remarks both apply to the situation simulated in Fig. 5 and emphasize the properties that the new model and AYALA's experiment have in common. As a conclusion, AYALA (1969) stated that the Volterra equations did not give an adequate description of the competition between two drosophilid species. This conclusion may be generalized by stating that, if the Volterra equations describe competition between species having a continuous development, they cannot account for species with CLCs, i.e. for species

having different competition coefficients depending on the stase. However, a slight modification of the original model, i.e. the introduction of a minimal age-class structure based on the stase concept, yields significantly more accurate results and allows the Volterra equations to account for species with CLCs. Therefore, the new model is preferred to other more sophisticated models which have been designed to explain AYALA's data but do not consider the discrete ontogeny observed in insects and other arthropods (GILPIN and JUSTICE, 1972 ; GILPIN and AYALA, 1973 ; AYALA *et al.*, 1973).

CONCLUSIONS

The approach outlined in this paper shows that the development through stases observed in arthropods may, under some conditions, lead to densities which are, for certain stases, well below their respective carrying capacities. As a result, habitats are not necessarily saturated by a given stase.

Due to the non-saturation of habitats by certain stases, the risk of competition between these stases is reduced.

Consequently, the probability of coexistence between species arises with the complexity of development. Two extreme cases are illustrated in Fig. 1 where an ontogeny composed of two similar instars (Fig. 1A) is compared to an ontogeny comprising two quite different stases (Fig. 1B). The outcomes of competition between species with instars (i.e. between age-structured populations) are those predicted by the Gause model. In contrast, the introduction of a minimal stase structure into the Gause model has remarkable consequences since the number of possible equilibrium points increases. As summarized in Table 3, coexistence is all the more probable as the ontogenies become more complex. In this approach, the unit of selective competition is not the species any more, but the stase.

Inasmuch as closely related species are likely to compete, a taxon with complex ontogenies should be more diversified than a taxon with simple development. In primitive insect groups, stases are little differentiated. This is the case in Collembola where stases are very similar except for the first one which may, in some species, occupy an ecological niche quite different from that colonized by older stases. The number of species in Collembola is much lower than that observed in more evolved groups. Most evolved insect orders, such as Coleoptera, in which CLCs and metamorphoses occur, are in fact, extremely speciose. Ontogenies in most evolved groups may become very complex and involve hypermetamorphoses, the presence of several calyptostases (non-feeding and non-walking forms supposed to have low competitive abilities), the heteroxeny observed in many parasites or the alternation of heteromorphic generations as in heterogony.

In conclusion, a new hypothesis is proposed to explain the role and function of CLCs in insects and other arthropods. Metamorphosis and other life cycle complexities observed in arthropods may have developed as an inevitable effect of minimizing constraints due to competition between species living in the same habitat. This minimization of interspecific competition has allowed arthropod species to

diversify to an extreme degree. Although metamorphosis and competition are seemingly unrelated concepts, the former appears to be a way of minimizing the latter and is a prerequisite to the fabulous diversity found in arthropods. This hypothesis supplements SOUTHWOOD's (1978) views mentioned in the introduction but strongly disagrees with MAY's (1978) opinion that the limits to similarity and niche overlap have little to do with the relative diversity of insect faunas.

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