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## A new formulation for determination of the competition coefficient in multispecies interaction for Lotka–Volterra type competition models

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**Determination of competition coefficients constitutes a vital part in the competition-based Lotka–Volterra-type population dynamics models. Various models have been proposed for the same, some of which were instinctive formulations, while some others were**

**derived from dynamical and equilibrium relations pertaining to population dynamics. In this work, a new instinctive formulation to determine the competition coefficient has been proposed based on various parameters that determine the intensity of interspecific competition like the availability of resources, relative importance of a particular resource for a species, energy expenditure per resource utilization, etc.**

**Keywords:** Competition, interspecies interaction, niche overlap, resource utilization.

THE study of interspecific competition amongst species has been one of the most prevalent concerns in the field of ecology, since the conception of competition. Most of the early evidence was forged on the basis of observational cues and limited laboratory experimentation (that too under constrained circumstances), rather than on-the-field studies<sup>1</sup>. This led to the questioning of the very principle of competition being a major force in population dynamics, especially in the 1960s–80s, resulting in a surge of experiments to prove or disprove the idea.

Most of the attacks were invalidated, but not without the amendment of the original theory of competition<sup>1</sup>. Schoener<sup>1</sup> reviewed about 164 experiments and discussed the results, which showed that interspecific competition occurred consistently in different habitat types and also at varied trophic levels as predicted by the theory. However, these experiments were designed to minimize the effect of predation, and thus did not account for the predatory effect. Later, Sih *et al.*<sup>2</sup> and Gurevitch *et al.*<sup>3</sup> analysed numerous experiments which had taken both predation and competition into account. This analysis demonstrated predation as a stronger effect, but nevertheless confirmed competition as a powerful factor in the interactions of multiple species<sup>2</sup>. Even today, numerous experiments<sup>4,5</sup> and simulations<sup>6</sup> demonstrate the importance of interspecific and intraspecific competition in modelling the dynamics of populations and their evolution.

The equations for interspecific competition, as suggested by Volterra<sup>7</sup> and later expounded by Lotka and Gause<sup>8</sup>, which form the basis of our discussion, are of the general linear form (for  $n$  species)

$$\frac{dN_i}{dt} = r_i N_i \left[ 1 - \frac{\sum_{j=1}^n \alpha_{ij} N_j}{K_i} \right], \quad (1)$$

where  $n$  is the total number of interacting species,  $N_i$  the population size of species  $i$ ,  $K_i$  the carrying capacity of species  $i$ ,  $\alpha_{ij}$  the competition coefficient of species  $i$  due to species  $j$  and  $r_i$  is the intrinsic growth rate of species  $i$ . Here, the competition coefficient is a key phenomenological measure of the interspecific interaction and serves an important part in the modelling of actual dynamics. (Note that nonlinear forms of these models also exist.)

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The element of the  $n$ -species interaction models which forms the basis of this work is the competition coefficient, usually denoted by the symbol  $\alpha_{ij}$ , signifying the competition between species  $i$  and  $j$ . It is defined as a measure of the extent to which an individual of a species influences the growth or stability of the population of a second species, through competition, compared to the influence of an individual of the latter<sup>9</sup>. There have been numerous models in the past to estimate the competition coefficient from laboratory data, field data, or other indirect sources. Estimation of the coefficient  $\alpha_{ij}$  is usually done by fitting the dynamic form of population equation to data from experiments<sup>8,10</sup>, using equilibrium states of resource–consumer versions of the Lotka–Volterra equations<sup>9,11–17</sup> or using simulative techniques<sup>3</sup>. The problem that we will be dealing with here is to construct an alternate model for determining the competition coefficient, and also to overcome some of the shortcomings of the earlier formulations, which have been described below.

MacArthur and Levins<sup>11</sup> were the first to propose a mathematical formulation relating resource utilization spectra and competitive intensity, expressing the fact that competition coefficient could be calculated as a degree of ecological overlap<sup>1</sup>. This coefficient was defined to be the competitive effect on the growth of species  $i$  of an individual of species  $j$ , divided by the same effect of an individual of species  $i$ . Mathematically

$$\alpha_{ij} = \frac{\sum_h p_{ih} p_{jh}}{\sum_h p_i h^2}, \quad (2)$$

where  $p_{ih}$  in the most general sense indicates the relative resource utilization calculated as a fraction of the total use of all resources for competitor  $i$ , of the resource  $h$  by competitor  $i$ .

Several experiments demonstrated that low ecological overlap was linked with low competition, and vice versa<sup>18,19</sup>. Later it was found that pronounced ecological overlap need not show great competition but may result from interspecific tolerance, whereas low overlap may be caused from aggressive exclusion<sup>1,13,20</sup>, amid additional effects. Numerous ecologists have found eq. (2) above quite handy, regardless of these potential difficulties.

The form that MacArthur discusses mostly involves a method where he modifies the Lotka–Volterra prey–predator system by adding some terms to change them into the form of resource–consumer interaction, and solves the equations for equilibrium conditions in order to estimate the value of  $\alpha_{ij}$  which can be represented in the following form<sup>11,21</sup>

$$\alpha_{ij} = \frac{\sum_{k=1}^s a_{ik} a_{jk} \left( \frac{b_{ik} K_k}{r_k} \right)}{\sum_{k=1}^s a_{ik}^2 \left( \frac{b_{ik} K_k}{r_k} \right)}, \quad (3)$$

where  $a_{ik}$  is the consumption rate of resource  $k$  by competitor  $i$ ,  $b_{ik}$  the net energy per item of resource  $k$  that can be assimilated or used by an individual competitor  $i$ ,  $K_k$  the carrying capacity of resource  $k$  in the absence of predation,  $r_k$  the intrinsic growth rate of the resource  $k$ , and  $s$  is the total number of resources. This formulation assumes that consumers come across resource types in keeping with their proportions in the whole system (or assumes some other encounter process that aggregates to this situation)<sup>1</sup>. This assumption would be violated if the resource types are particular macro-habitats, especially where territorial competition is present<sup>1</sup>, however, the formulation is quite useful as other than this problem it takes care of other shortcomings of eq. (2). According to this formulation, the larger the consumption rate of species  $j$  with respect to species  $i$ , larger would be the value of  $\alpha_{ij}$ .

Field data can be used in this expression in order to calculate  $\alpha_{ij}$ , as suggested by MacArthur<sup>21</sup> within the assumptions as mentioned above. Also, under some simplifying assumptions, i.e. the ratio  $b_{ik} K_k / r_k$  being equal for all  $k$  resources, eq. (3) can be simplified into eq. (2).

However, none of these takes into account the abundance of the resource being used. Moreover, if the ‘resource-use composition’ for different species, and the total resource magnitude in a given area are known,  $\alpha_{ij}$  can still be computed, but not by replacing various parameters in eqs (2) and (3). Schoener<sup>9</sup> suggested that if the ecological system is studied at equilibrium, then for an individual in species  $i$ , the quantity of items  $n_{ik}$  that it uses of the resource  $k$ , is a product of two quantities: ‘per-unit-resource rate of consumption’ ( $a_{ik}$ ) and the total magnitude of resource ( $\hat{F}_k$ ). Then

$$a_{ik} = \frac{n_{ik}}{\hat{F}_k} = \frac{d_{ik} \sum_k n_{ik}}{f_k \sum_k \hat{F}_k}, \quad (4)$$

where  $d_{ik}$  is the proportion of resource  $k$  used by species  $i$  in its diet,  $d_{ik} = n_{ik} / \sum_k n_{ik}$  and frequency of resource in the environment  $f_k = \hat{F}_k / \sum_k \hat{F}_k$ . Now on substituting eq. (4) into eq. (3), we obtain a relation which no longer depends on  $\sum_k \hat{F}_k$ , the total number of items of all resources

$$\alpha_{ij} = \frac{\left( \sum_k n_{jk} \right) \sum_{k=1}^s (d_{ik} / f_k) (d_{jk} / f_k) (b_{ik} K_k / r_k)}{\left( \sum_k n_{ik} \right) \sum_{k=1}^s (d_{ik} / f_k)^2 (b_{ik} / f_k)^2 (b_{ik} K_k / r_k)}. \quad (5)$$

These models of determining the value of  $\alpha_{ij}$  are usually proposed so that its value can be calculated independently using field measurements. However, there are certain shortcomings associated with each of these models, in addition to the ones discussed above.

The biggest problem with most of these models is the fact that they result in constant coefficients, which are actually far from reality, as the intensity of competition also depends on the size of the population at a given instant of time. The only factor that may result in ‘changing’ coefficients in the above formulations is  $f_k$ , which may result in a change in  $d_{ik}$ , but that is not usually incorporated. Some of the assumptions that underlie these models have been discussed by Abrams<sup>22</sup>, especially for the MacArthur formulations and their derivatives, which he enlists as follows:

1. There is competition for a number of resources among multiple consumer species and all the resources replenish in accordance to the logistic equation.
2. The amount of resources that an individual consumes in a given time is a linear function of resource densities.
3. Per capita growth rates of the consumer populations are linear functions of the extent of resources consumed.
4. Homogeneity is assumed for all consumers and resources, resulting in no genetic or size/age-specific variation in the utilization of resources.
5. Population processes for the resource populations happen at rates much rapid than the processes in consumer population. (This assumption is not explicit, but is taken in order to solve the differential equation of the resources at a steady state.)
6. The consumers do not drive their resources to extinction.
7. No lag exists in the consumer’s population response to resource densities.
8. There is no interaction among the resources.

These assumptions take the models away from most natural systems, whose implications are discussed by Abrams<sup>22</sup>. The biggest drawback of the MacArthur formulations remains that the coefficients are constant in time. Also, it assumes that populations are uniform and consume resources in a given uniform environment; and that there is no age/size variation in consumption<sup>22,23</sup>. In addition, extinction of at least one of the resources is probable if there is an increase in the number of resources consumed<sup>16</sup>. In the present formulation, some of these assumptions are taken care of, at least to some extent. Discussions about the implications of these formulations will be done later in this work.

The present formulation is based on the same basic idea that an increased overlap of resource utilization spectra also results in high competition among the species concerned. But instead of measuring or even devising ways to measure the actual overlap, it focuses on the availability and importance of a given resource for a species. The formulation has a few parameters that simplify the concept of competition, and are described below.

Interspecific Niche overlap (denoted by  $\delta_{ij}$ ) – There will be competition between any two species, given that there is an overlap between their niche volume ( $\mathbb{V}$ ) in  $K$ -dimensional space (given there are  $K$  resources), where each of the dimensions represents a niche parameter, i.e. a resource in this case. These parameters can be divided into two categories: the inconsumable parameters, which can be defined as the entities that do not get depleted on being used by one individual, like temperature, humidity, etc. and consumable parameters which get depleted on consumption like food, water, etc. In this model we work with only consumable parameters, assuming that the species share a common habitat.

To avoid all the confusion regarding calculation of the volume, we consider each parameter/resource individually. The basic idea is that if a particular resource is being utilized by both the species, then it will play a role in the competition coefficient directly; otherwise, it will not. If there is a resource  $\beta$  which both species use, in other words  $(\mathbb{V}_{i\beta} \cap \mathbb{V}_{j\beta}) \neq 0$ , then it will contribute to a summand in the calculation of  $\alpha_{ij}$ . So, we can define

$$\delta_{ijk} = \begin{cases} 1, & \text{if } (\mathbb{V}_{ik} \cap \mathbb{V}_{jk}) \neq 0, \\ 0, & \text{if } (\mathbb{V}_{ik} \cap \mathbb{V}_{jk}) = 0. \end{cases} \quad (6)$$

Energy efficiency ( $\mathcal{E}_{ik}$ ): This is defined in the following way

$$\mathcal{E}_{ik} = \frac{\langle \mathbb{E}_{ik}^g \rangle - \langle \mathbb{E}_{ik}^s \rangle - \langle \mathbb{E}_{ik}^a \rangle}{\langle \mathbb{E}_{ik}^s \rangle}, \quad (7)$$

where  $\langle \mathbb{E}_{ik}^g \rangle$  is the energy gained due to an item of the resource type  $k$ ,  $\langle \mathbb{E}_{ik}^s \rangle$  the energy required for searching an item of the resource type  $k$ , and  $\langle \mathbb{E}_{ik}^a \rangle$  is the energy required for catching and processing the same.

$\langle \mathbb{E}_{ik}^s \rangle$  can be calculated by first finding the average time required for an individual of species  $i$  to search for an item of resource type  $k$ , and then multiplying it with the average energy spent per unit time.

$\langle \mathbb{E}_{ik}^a \rangle$  maybe calculated by finding the energy spent in catching, handling and assimilating the resource, which can be found using a similar procedure as for  $\langle \mathbb{E}_{ik}^s \rangle$ .

Resources like water, land, etc. from which energy cannot be assimilated are assumed to be abundant enough so as to not influence the competition coefficient.

The aforesaid energy usage rates that are used to calculate  $\langle \mathbb{E}_{ik}^s \rangle$  and  $\langle \mathbb{E}_{ik}^a \rangle$ , can be inferred using accelerometer techniques<sup>24</sup>. The field metabolic rates have been previously calculated using labelled (heavy) water method for multiple species<sup>25,26</sup>. These studies calculated the average daily usage of energy for the organisms. With the current techniques involving accelerometer, movement paths, energy spent per unit time, rate of energy gain for a given prey type, and assimilation efficiency can be calculated for various situations<sup>27–29</sup>.

The energy required to find and catch a prey can vary from situation to situation. In the calculation of  $\langle \mathbb{E}_{ik}^s \rangle$  we utilize the energy used per time unit by the animal to prey. This energy usage will depend exceedingly on circumstance, and hence cannot be assigned a certain value. Thus, in this model we intend to use estimates obtained as explained above rather than specific values. While implementing these values to run the model, the actual of  $\mathcal{E}_{ik}$  could be picked randomly from a normal distribution with its mean as the value we estimated for  $\mathcal{E}_{ik}$  each time it is required.

*Resource usage coefficient ( $\mathcal{A}_{ik}$ ):* To incorporate how important a given resource is for an individual, the resource usage coefficient is used as a parameter, which is defined as

$$\mathcal{A}_{ik} = \frac{\mathcal{E}_{ik}}{\sum_l \mathcal{E}_{il}}. \tag{8}$$

The resource usage coefficient also gives us a brief idea about the diet of the individual. On finding the value of  $\mathcal{A}_{ik}/\sum_q \mathcal{A}_{iq} = \mathcal{E}_{ik}/\sum_q \mathcal{E}_{iq}$  where all the  $q$  resources are dietary, we can find the proportion of resource in the diet. From this we can estimate its average diet composition and vice versa.

If a resource is too scarce, its  $\mathcal{E}$  value decreases considerably and thus its importance decreases even though it may be quite profitable. So, not only the energy content of the resource but also its availability for use would also be important.

In this model we have considered that the animals will consume resources proportional to their energy efficiencies. The rationale behind this is the greedy algorithm. The more a resource is energy-efficient, the more it should be consumed by the animals. This begs the question: why do the animals not opt for the most energy efficient resource only?

If all the animals would opt for the most energy-efficient resource, the competition for it would be large, and it would start to dwindle. Moreover, consuming only the most energy-efficient resource would imply more search time for the animals, as the resource would be spread out in a wide area. Whereas if the animal were to divide its energy requirements among several resources it would make for a lower search area thus reducing the energy spent for searching.

*Estimated resource requirement ( $\hat{Q}_{ijk}$ ):* This is the estimated amount of resource of type  $k$  required by the current population of both species  $i$  and  $j$  combined. To begin with, we find  $\hat{Q}_{ijk}$  using field data of the estimated current population sizes of both the species, i.e. we use  $N_i$  and  $N_j$  and the periodic resource requirements, i.e.  $\mathcal{P}_{ik}$  and  $\mathcal{P}_{jk}$ . Then we calculate  $\hat{Q}_{ijk}$  as  $\hat{Q}_{ijk} =$

$N_i \mathcal{P}_{ik} + N_j \mathcal{P}_{jk}$ . This value of  $\hat{Q}_{ijk}$  is then used in the discrete Lotka–Volterra model (described later in the text) to predict values of  $N_i$  and  $N_j$  for the following year. With these values of  $N_i$  and  $N_j$ ,  $\hat{Q}_{ijk}$  is determined again and updated in the model to predict subsequent population values.

*Estimated total resource quantity ( $\hat{T}_k$ ):* This is the total amount of resource of type  $k$  found in a given area where the population dynamics is being studied at that time. It can be estimated either using large-scale field data collection or by small-scale sampling followed by estimation.

*Periodic resource requirement ( $\mathcal{P}_k$ ):* This is the total amount of resource of type  $k$  required by species  $i$  in a specific period of time. This factor is not the same as the  $a_{ik}$  used in the literature<sup>11,16,21</sup>, because when the logistic model is applied to MacArthur and similar formulations, we consider the consumption rate of a resource  $k$  by species  $i$  to be linearly related to the resource density of resource  $k$ , whereas  $\mathcal{P}_{ik}$  is the total requirement of the resource  $k$  by species  $i$  irrespective of the resource density (if and only if  $\hat{T}_k \geq \hat{Q}_{ijk}$ ).

Many field studies have found the dietary composition of various organisms from which the value of  $\mathcal{P}_{ik}$  can be calculated<sup>30,31</sup>.

The expression for  $\alpha_{ij}$  using various parameters discussed above can be written in the following general form

$$\alpha_{ij} = \sum_k \delta_{ijk} \mathcal{A}_i \left( \frac{\hat{Q}_{ijk}}{\hat{T}_k} \right) \left( \frac{\mathcal{P}_{jk}}{\mathcal{P}_{ik}} \right). \tag{9}$$

Equation (9) states that for a particular resource  $\beta$ , if  $(\mathbb{V}_{i\beta} \cap \mathbb{V}_{j\beta}) = 0$ , then there is no competition between species  $i$  and  $j$  for that particular resource making that summand, i.e.

$$\delta_{ij\beta} \mathcal{A}_{i\beta} \left( \frac{\hat{Q}_{ij\beta}}{\hat{T}_\beta} \right) \left( \frac{\mathcal{P}_{j\beta}}{\mathcal{P}_{i\beta}} \right)$$

is zero. On the other hand, if  $(\mathbb{V}_{i\beta} \cap \mathbb{V}_{j\beta}) \neq 0$  for  $\beta$ , then the summand is not zero; in fact

$$\delta_{ij\beta} \mathcal{A}_{i\beta} \left( \frac{\hat{Q}_{ij\beta}}{\hat{T}_\beta} \right) \left( \frac{\mathcal{P}_{j\beta}}{\mathcal{P}_{i\beta}} \right) = \mathcal{A}_{i\beta} \left( \frac{\hat{Q}_{ij\beta}}{\hat{T}_\beta} \right) \left( \frac{\mathcal{P}_{j\beta}}{\mathcal{P}_{i\beta}} \right) \neq 0 \text{ as } \theta_{ij\beta} \text{ is } 1.$$

The term  $\mathcal{A}_{ik}$  states the importance of the resource  $k$ , for the existence of species  $i$  in a given environment with respect to its dietary composition, i.e. resource requirements. This is vital because a resource important for the species in general might be scarce in some environments

and consequently, if other equivalent resources are available, its significance reduces considerably. It is essential to note that this term is a function of time as it also incorporates the seasonal variation of abundance as well as the temporal variation of a resource due to external constraints.

The next term  $\widehat{Q}_{ijk}/\widehat{T}_k$  in eq. (9) describes the intensity of competition by directly incorporating the information about scarcity. When  $\widehat{Q}_{ijk}$  is much less than  $\widehat{T}_k$ , the level of competition reduces and the dynamics changes to something similar to the exponential form of growth. It is to be noted that the expression for  $\alpha_{ij}$  is also valid for intraspecific competition ( $\alpha_{ii}$ ), which also tends to zero when  $\widehat{Q}_{iik}/\widehat{T}_k$  tends to zero, resulting in the exponential growth expression.

The final term  $\mathcal{P}_{jk}/\mathcal{P}_{ik}$  in eq. (9) describes the ratio of requirement of resource of type  $k$ . This term incorporates the interspecific interaction in particular, describing the need for the resource by the other species given that all other parameters are equivalent.

A question which may arise is that if one of the resources dwindles toward extinction, will the system of equations fail? However, this is also taken care of by the factors that precede the resource availability coefficient in the formulation. Suppose one particular resource, say  $\beta$ , dwindles and its quantity goes to zero, i.e. the term  $\widehat{T}_\beta$  goes to 0. The question is what happens to the summand containing  $\beta$ ; in other words, what happens to

$$\delta_{ij\beta} \mathcal{A}_{i\beta} \left( \frac{\widehat{Q}_{ij\beta}}{\widehat{T}_\beta} \right) \left( \frac{\mathcal{P}_{j\beta}}{\mathcal{P}_{i\beta}} \right).$$

Ecologically speaking, this term should go to zero as the contribution from that resource should disappear. Observe that as  $\widehat{T}_\beta$  goes to zero,  $\mathcal{A}_{i\beta}$  will go to zero. This is because the dietary contribution of  $\beta$  will also go to zero ( $\delta_{ij\beta}$  is 1). For as long as  $\widehat{T}_\beta \geq \widehat{Q}_{ij\beta}$ , the third term, i.e.  $(\widehat{Q}_{ij\beta}/\widehat{T}_\beta)$  is less than 1, and the fourth term, i.e.  $(\mathcal{P}_{j\beta}/\mathcal{P}_{i\beta})$  is a constant. When  $\widehat{Q}_{ij\beta}/\widehat{T}_\beta$ , then the values of  $\mathcal{P}_{j\beta}$  and  $\mathcal{P}_{i\beta}$  will change. This is true since, if the particular source is dwindling, the consumption rate will decrease for the species, as it will try to recompense from other food sources. The critical point before this starts to happen will be when  $\widehat{Q}_{ij\beta} = \widehat{T}_\beta$ . If  $\widehat{T}_\beta$  further decreases, then  $\widehat{Q}_{ij\beta}$  will adjust itself by means of changing values of  $\mathcal{P}_{j\beta}$  and  $\mathcal{P}_{i\beta}$ , so that  $\widehat{Q}_{ij\beta} = \widehat{T}_\beta$ . Thus, the term  $\widehat{Q}_{ij\beta}/\widehat{T}_\beta$  will remain close to 1. Hence the total summand, i.e. the product of all these terms will go to 0, as  $\mathcal{A}_{i\beta}$  goes to 0, and all the other terms have finite bounds.

In most other previous formulations (and the most simplified form of the equations),  $\alpha_{ii}$  has been taken to be 1. However, this is only for the equilibrated case. So, to keep the equations consistent with previous formulations

at least using this common point of reference, we have at equilibrium the value of  $\alpha_{ii}$  to be 1. From our formulation for one resource, say  $\beta$ , we have

$$\alpha_{ii} = \delta_{ii\beta} \mathcal{A}_{i\beta} \left( \frac{\widehat{Q}_{ii\beta}}{\widehat{T}_\beta} \right) \left( \frac{\mathcal{P}_{i\beta}}{\mathcal{P}_{i\beta}} \right). \tag{10}$$

Here,  $\delta_{ii\beta} = 1$ , as a single resource is being used by species  $i$ .  $\mathcal{A}_{i\beta} = 1$ , as we consider a single resource.  $\mathcal{P}_{i\beta}/\mathcal{P}_{i\beta} = 1$  (obviously as the terms cancel out).  $\widehat{Q}_{ii\beta} = \mathcal{P}_{i\beta} N_i$  as here we consider a single population of species  $i$ .

Hence at equilibrium  $\widehat{Q}_{ii\beta} = \mathcal{P}_{i\beta} K_i$  this is the carrying capacity of the species multiplied by its consumption rate, which is nothing but  $\widehat{T}_\beta$  at equilibrium. This can be thought of as the point where the ecosystem has just enough resources of type  $\beta$  so that it can sustain a population of species  $i$  when it has reached its maximum population value.

Hence the term  $(\widehat{Q}_{ii\beta} = \widehat{T}_\beta)$  is also 1. Thus at equilibrium

$$\alpha_{ii} = \delta_{ii\beta} \mathcal{A}_{i\beta} \left( \frac{\widehat{Q}_{ii\beta}}{\widehat{T}_\beta} \right) \left( \frac{\mathcal{P}_{i\beta}}{\mathcal{P}_{i\beta}} \right) = 1. \tag{11}$$

The question arises, why is  $\widehat{T}_k$  used instead of  $K_k$  and  $r_k$  (which were used in the previous formulations)? We are interested in the total amount of resource present in terms of biomass per resource, rather than the carrying capacity of the same. Since we are using the discrete Lotka–Volterra model, our aim is to observe and incorporate in our formulation the total available amount of a particular resource to be used by the two competing species. While  $K_k$  and  $r_k$  give us an estimate of resource availability, we are more concerned with the actual available resource. Hence we use the field/satellite data for the amount of available resource per resource. Moreover,  $K_k$  and  $r_k$  are difficult to measure empirically compared to direct field/satellite observations of the resource quantity.

It has to be noted that the coefficient for given time-point can be estimated here using the parameters, which in turn can be estimated using the values of populations at the previous time-point. This can be repeated a few times in order to get a good bound on the value of the coefficient at the time-point.

The ultimate aim of this study is to estimate the population size of a species after some time-period. We achieve this using the Lotka–Volterra equation; but to do so we need to estimate the coefficient  $\alpha_{ii}$ . From our model, for which we need to estimate the following at a given time point say  $t$ :

- $\widehat{T}_k$  for every resource. This factor is time-dependant.
- $N_i$  and  $N_j$ , i.e. population sizes of both the species. These are also time-dependent.

- $\mathcal{P}_{ik}$  and  $\mathcal{P}_{jk}$  for every resource. These factors are time-independent (this is of course an assumption, but one we believe to be quite reasonable, as the minimum required amount of food needed for an individual of a given species is almost a time invariant), for as long as  $\hat{\mathbb{T}}_k \leq \hat{\mathbb{Q}}_{ijk}$ . However, complications arise because of variation in food habits due to altering food densities, especially in the region  $\hat{\mathbb{T}}_k \leq \hat{\mathbb{Q}}_{ijk}$ .
- $\langle \mathbb{E}_{ik}^g \rangle$ ,  $\langle \mathbb{E}_{ik}^s \rangle$  and  $\langle \mathbb{E}_{ik}^a \rangle$  for every resource. Again, we assume that these are time-independent quantities.

So, we use the discrete Lotka–Volterra model and the values mentioned above to calculate  $\alpha_{ij}$  and hence obtain  $N_i$  for the time-step  $T = t + 1$ , and similarly obtain  $N_j$  for time  $T = t + 1$ .

Then from field data we can update the values of  $\hat{\mathbb{T}}_k$  for time,  $T = t + 1$ , and use  $N_i$ ,  $N_j$  and  $\hat{\mathbb{Q}}_{ijk}$  (calculated using  $N_i$ ,  $N_j$  for time  $t + 1$  and the constants  $\mathcal{P}_{ik}$  and  $\mathcal{P}_{jk}$ ) for time,  $T = t + 1$  to calculate  $\alpha_{ij}$  for time  $= t + 1$ . Iterating this procedure gives us a good estimate of the population growth of both the species over a given period of time. Reducing the time-period of iteration will further better the estimate of the population size after a given time.

A typical usage of this model would be in the case of modelling populations in the grasslands. In this case, it is easier to predict the vegetation cover and distribution based on abiotic cues<sup>23</sup>, rather than to find the populations directly. Another such example is the phytoplankton density in oceans, where the total resource is easily predictable<sup>32</sup>. In many cases, the value of resource availability has been tabulated over a long period of time, obtained using satellites and fitted into a predictive model<sup>33</sup>.

In addition, as pointed out by Schoener<sup>34</sup>, some models formulated different from Lotka–Volterra systems favour more coexistence<sup>9,35,36</sup> by ensuring the fact that rarer a given species more the individuals of a second species are needed to decrease the equilibrium population of the rarer species by a fixed amount. This dynamics also depends on the resource requirement and the actual availability. The coefficient determination as discussed in this work, displays a little of the property mentioned above. This was not present in previous formulations of coefficient determination.

There are a fewer assumptions inherent in this formulation, compared to those discussed by Abrams<sup>22</sup>. These pose some restrictions to the formulations, but still it would be applicable in most of exploitative competition cases, but not in direct predator–prey interactions. When one compares the shortcomings of the previous formulations which could be rectified using the present model, we can summarize the outcome as follows.

1. The parameter  $\hat{\mathbb{T}}_k$  in the present formulation may be represented by real-time field data, or can also be modelled using the logistic equation. The older formulations

use the parameters  $K$  and  $r$  so as to model the logistic growth of resources, while the present formulation uses the total available resource data (from field) as a parameter in the model. Due to the use of real-time data taken after every time-interval, we can take into account the fluctuations of the availability of the resources due to environmental changes. This cannot be done when parameters  $K$  and  $r$  are being used. Thus, it corrects the shortcoming of the exclusive use of logistic equations for the computation.

2. The individual resource consumption parameter in the present formulation, i.e.  $\mathcal{P}_{ik}$ , as mentioned previously is independent of the total resource densities and thus solves the problem associated with the previous formulations (which assumed that the amount of resources that an individual consumes in a given time is a linear function of resource densities).

3. Here we model the competition coefficient for the non-consumer–resource-type Lotka–Volterra equations, where we use the parameter  $r$  which is half the average reproductive rate per individual (because a pair of individuals is responsible for the reproduction and hence taking  $r$  as the full reproductive rate would mean to wrongly double count), and hence avoid the case of using the prey–predator-type model and its assumption that per capita growth rates of the consumer populations are linear functions of the extent of resources consumed.

4. Also, the assumption in the older formulations that the consumers do not drive their resources to extinction has been taken care of specifically.

5. In the present formulation, we can model the genetic and age variability using the distribution of these various groups in the population in the previous iteration of the population calculation to evaluate a weighted value of different parameters like  $\mathcal{P}_{ik}$ ,  $\hat{\mathbb{Q}}_{ijk}$ , etc.

6. The assumption that there is no interaction among the resources does not exist in the present formulation as the direct field values of resource populations are taken at different time-points which enable the modelling of resource interactions indirectly, without explicitly calculating them.

Furthermore, eq. (9) can also describe the competition with a species, where different age groups can be considered as sub-divisions of the species. This property of eq. (9) can therefore be used to model the intraspecific dynamics of a species in a more realistic way. A direct comparison with other models might prove to be really difficult because some of the major parameters differ in the formulations.

The expression for  $\alpha_{ij}$  as described in eq. (9) may prove to be demanding for calculation, but the parameter estimation may be improved in order to achieve better computation. Even though there are quite a few parameters, their computation may not actually be as difficult, if we incorporate the fact that we would calculate them from the field data. The whole process might be

resource-intensive (for data collection), but it would give a better view of the competition coefficient without having been computationally intensive. Equation (9) models many aspects of intraspecific competition, along with the resource availability parameters, and thus gives a representative value for the competition coefficient  $\alpha_{ij}$ , which varies both temporally and spatially as is represented in most natural systems. Thus, improving upon such an expression might prove to be useful in accurately modelling the population dynamics in natural conditions.

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