An extension of some classic results on species competition in structured habitats

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We extend some results on population dynamics in a structured habitat, obtained in a classic paper by J.G. Skellam [1], regarding competition between two species differing in fitness, in a habitat with two unequal sectors. Using the discrete spatial and temporal method introduced by him, we generalize his results to an arbitrary number of species ranked according to fitness, competing in a habitat with any number of sectors. We show particular instances of complete species segregation, and of segregation in some sectors, and coexistence in others. We also consider the case of two species, when fitness superiority is not absolute in the sense originally defined by Skellam. Then we briefly ponder the relevance of his discrete method to subsequent research, based on a survey of the fundamental literature on this subject.

Keywords: Ecosystems; species propagation; structured habitat; metapopulation; niche.

Generalizamos algunos resultados sobre dinámica de poblaciones en un hábitat estructurado, obtenidos en un trabajo clásico de J.G. Skellam [1], sobre competencia entre dos especies que difieren en su grado de adaptación a un hábitat compuesto de dos sectores distintos. Usando el método espacial y temporalmente discreto introducido por Skellam, extendemos sus resultados al caso de un número arbitrario de especies con distintos grados de adaptación, en un hábitat compuesto de múltiples sectores. Ilustramos por medio de ejemplos particulares las alternativas de segregación total de las especies, y de segregación en algunos sectores y coexistencia en otros. Analizamos además el caso de dos especies, cuando la superioridad de la mejor adaptada entre ellas no es absoluta en el sentido originalmente definido por Skellam. Ponderamos brevemente a continuación la relevancia de su método discreto en investigaciones posteriores, basados en un análisis de la literatura fundamental sobre este tema.

Descriptores: Ecosistemas; propagación de especies; hábitat estructurado; metapoblación; nicho.

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1. Introduction

In a remarkable paper on animal and plant propagation in ecosystems, J.G. Skellam [1] introduced half a century ago concepts and methods close to those employed in modern theories on the same subject. His main contribution to this problem, namely a continuum (diffusion) scheme supplemented with source terms and a sink supplied by hostile surroundings, has become a classic in this field, making him the "father of ecological diffusion" [2,3].

Less well known is his discrete approach (both in space and time) to the question of species competition in structured habitats, near the end of the same paper. In it, he first calculated the stationary population of a single plant species in a homogeneous habitat, whose individual members show finite mortality. He then analyzed the case of two closely related species, a strong and a weak one, competing in a single, homogeneous habitat. He concluded that, if they are able to persist alone, they also coexist under certain conditions, as members of the weaker species survive occupying sites left over by those from the stronger one, due to mortality. Finally, he considered the case of two species, a strong and a weak one, competing in a habitat comprising two different sectors, a rich and a poor one. He identified in this case a tradeoff between fitness and the number of offspring (or seeds produced), allowing the weaker, more prolific individuals, to persist in the poorer sector.

In this paper, we provide an extension of Skellam's results on species competition, and deal with an arbitrary number of species competing in a habitat composed of various patches spanning a range of suitability. We also consider the case of non-absolute superiority when two species differing in fitness compete. Then we briefly consider the connection of Skellam's concepts and methods with current research on population ecology, including metapopulation models [4,5], and interspecific interactions [6,7].

In Sec. 1 we outline the main results in Skellam's paper regarding his discrete method, and provide in Sec. 2 the extension mentioned above. Section 3 briefly ponders the conceptual and methodological impact of Skellam's discrete approach on later work, through a survey of the fundamental literature on the subject.

2. Skellam's results on animal and plant propagation

Skellam's article [1] contains both a continuum and a discrete approach to the problem of species persistence and propagation. His continuum scheme is based on population gain through births, and loss through diffusion beyond habitat borders into a hostile environment. His mathematical description is based on a diffusion equation with a source term. His main result in this context was that a minimum habitat size is required for long therm persistence of a given species.
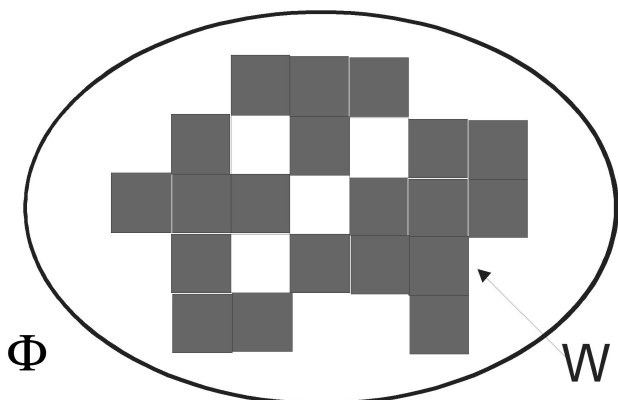
FIGURE 1. Skellam's ecological cells. Each square represents an area able to support one individual from seedling stage to maturity; shaded squares are full, and white ones (surrounded by shaded ones) are empty due to mortality; hence the habitat suitability factor s equals 5/6 in this case. The number of cells, $W = 24$, and the maximum number of adult plants that the habitat can carry, $Ws = 20$; Φ is an area large enough to contain all cells and receive no seeds from external sources; p is the fraction of seeds from inner cells that fall within Φ.

His discrete method deals with the problem of long-term plant persistence in a given habitat, considering the latter a collection of cells, each one able to support an individual from seedling stage to maturity (Fig. 1). He defines a long list of variables:

H, a compendium of factors that determine overall habitat suitability. In his approximation, $H = Wsp/\Phi$, where W is the number of cells, Φ an area that contains all the cells, and large enough so it receives no external seeds; p is the fraction of seeds that fall within the area Φ, and s the probabilitiy that a seeded cell rears a seedling to maturity; $s < 1$ thus implies mortality.

Γ denotes reproductive capacity, or the average number of seeds produced per plant.

χ indicates relative density, given by $\chi = N/Ws$, where N is the number of plants that reach maturity in each generation, and Ws represents the maximum number of them that the habitat does support.

He assumes that all cells are equally reachable by seeds, and considers synchronous generations, *i.e.*, all plants in a generation are born at the outset, and the surviving ones shed their seeds and then die out simultaneously. Under these approximations, he is led to a recursion relation for plant density in consecutive generations,

$$\chi_{n+1} = 1 - \exp(-\Gamma H \chi_n) \tag{1}$$

The stationary state condition, $\chi_{n+1} = \chi_n$, is attained in the limit $n \to \infty$; calling $\chi = \chi_\infty$, one thus has,

$$\chi = 1 - \exp(-\Gamma H \chi) \tag{2}$$

This equation implies $\Gamma H > 1$ as a requirement for long-term persistence (*i.e.*, $\chi > 0$).

Species competition. Skellam considers two closely related plant species (so the same individual cells are suitable for both of them), competing for occupation of a given habitat, with one of them showing definite superiority in fitness relative to the other. This means that whenever a seed from the stronger species (S) coincides in a cell with seeds from the weaker one (S'), the former always wins.

Under these conditions, the stronger species' fractional abundance (χ) is not affected by the presence of the weaker one. It thus satisfies Eqs. (1) and (2). The fraction of cells left over by members of S equals $(1 - \chi)$, and this is the portion available to members of S'. Defining $\chi' = N'/Ws$, one thus has, instead of Eq. (2),

$$\chi' = (1 - \chi)\left[1 - \exp(-\Gamma' H \chi')\right]. \tag{3}$$

From Eqs. (2) and (3), one gets the inequality,

$$\Gamma'/\Gamma > -\chi/(1 - \chi)\ln(1 - \chi), \tag{4}$$

as a requirement for the persistence of S', *i.e.*, for $\chi' > 0$. Hence there will be species coexistence (*i.e.*, both χ and χ' greater than zero), if condition (4) and $\Gamma H > 1$ are simultaneoulsy satisfied.

Based on these results, Skellam gives numerous examples of situations where species coexistence in a single habitat is possible. He then considers a composite habitat, with a rich sector and a poor one, and two species, a strong and a weak one. As the fractional population size depends only on the product ΓH, one can combine a high fertility value (large Γ), with a poor sector (small H), with the same effect on the corresponding fractional population as low fertility (small Γ), combined with a rich habitat (large H). Using this as a guide, Skellam provides particular examples of a weak, prolific species, being able to survive in the poorer sector of its habitat, when competing with a stronger, less prolific one, the latter persisting mostly in the richer sector.

3. Extension of Skellam's results

The above result by Skellam, regarding two species competing in a habitat with two sectors, can be extended to the case of n closely related species (so their individual members can survive alone in the same cells) competing in a habitat with m sectors, with arbitrary n and m. We assume that species can be ranked based on competitive strength, or fitness, obtaining a set $\{S_j\}$ with seeds or individuals from species S_i being unable to survive in the same cell with seeds or individuals from species S_{i-1}. Conversely, we rank habitat sectors in increasing order of richness, obtaining a set of values $\{H_k\}$, with $H_l > H_{l-1}$. The persistence condition for species i in habitat sector k, $\Gamma_i H_k > 1$, shows that weaker species will survive only if they are in addition prolific enough.

Following a trial and error strategy similar to that employed by Skellam in simpler cases, we were able to obtain various arrangements of species among available habitat sectors. We started in each case with the persistence condition, $\Gamma_i H_k > 1$, to find out which species were able to survive

TABLE I. Fractional population size of five species in a habitat comprising five different sectors. Γ_j indicates seed production by individuals from species j, in arbitrary units; H_i denotes the suitability, or richness, of habitat i, also in arbitrary units. Species are ranked according to dominance, the fittest species being also the least prolific one regarding seed production, and so forth. There is complete species segregation.

H	H_1	H_2	H_3	H_4	H_5
Γ	0.01	0.0024	0.00083	0.00049	0.00035
Γ_x 400	0.9801	0	0	0	0
Γ_y 1200	0	0.9316	0	0	0
Γ_z 2000	0	0	0.6725	0	0
Γ_4 2800	0	0	0	0.4881	0
Γ_5 3600	0	0	0	0	0.3821

TABLE II. Three species coexisting in a homogeneous habitat, with the indicated fractional population sizes. Γ_j and H denote seed production and habitat suitability, respectively; fitness decreases as one goes down the first column.

H	H
Γ	0.01
Γ_x 140	0.511
Γ_y 400	0.3825
Γ_z 1140	0.0351

TABLE III. Two species competing in a habitat with three different sectors; the dominant species is again the least prolific one. They can only coexist in the intermediate sector regarding suitability; the fittest species takes over the richest sector, and the weaker, most prolific one persists alone in the poorest sector.

H	H_1	H_2	H_3
Γ	0.01	0.0032	0.001
Γ_x 400	0.9802	0.3873	0
Γ_y 2000	0	0.5988	0.7968

alone in each habitat sector. Then we applied the species competition relationship, $\Gamma_{i+1}/\Gamma_i > -\chi_i/(1-\chi_i)\ln(1-\chi_i)$, in descending order of fitness, to eliminate the weaker species that cannot survive in the face of competition. This led to

some interesting special cases, from a biological point of view:

(i) Complete species segregation. Consider five species able to share five habitat sectors, and rank species according to dominance, with S_1 the fittest one . Choosing the corresponding seed production parameters $\{\Gamma_i\}$ and habitat richness factors $\{H_k\}$ as shown in Table I, we get a configuration where only one species remains in each sector, with the weaker, more prolific ones occupying the poorer patches.

(ii) Coexistence of several species in a given habitat. Consider three species, each able to occupy a given habitat if left alone. Choosing the Γ and H values in Table II, they all coexist in this habitat with the indicated densities.

(iii) Segregation in some habitat sectors and coexistence in others. Table III gives an example of this situation.

By tinkering with the values of Γ_i and H_k, the above examples can be generalized to any number of species in any number of habitat sectors.

Our trial and error approach to specific examples of species distribution in habitat sectors is fairly efficient in practice (after becoming familiar with it through examples involving just a few species and sectors), when dealing with up to about 10 species and a comparable number of sectors simultaneously. For arbitrarily large sets of species and sectors, choosing the appropriate combination of habitat suitability $\{H_k\}$ and species fertility $\{\Gamma_i\}$ to obtain a preordained distribution of species among sectors involves lengthy tuning of parameters. For the special case of total species segregation, however, the amount of guesswork is greatly diminished following the procedure described in the appendix.

Non-absolute superiority. Skellam's definition of species superiority in absolute fashion is not realistic; for example, a seed from the superior species may arrive in a given cell when one from the weaker species has already germinated there, and so forth. Given the complexity of ecological interactions, it seems more natural to assume instead that, when seeds or plantules from a given species compete with their counterparts from another one, the former will survive with probability p less than unity, while the latter will do so with probability $q = 1 - p$.

Let us consider the case of two species in a homogeneous habitat, using primed variables for the weaker one. When $q = 0$, the habitat occupation fraction χ for members of the strong species satisfies Eq. (2) above, with $\Gamma H > 1$ for long-term persistence. When the second species is also present, one has in addition the coexistence condition, $\Gamma'/\Gamma > -\chi/(1-\chi)\ln(1-\chi)$.

When $q > 0$, there is no obvious way to extend Skellam's results to arbitrary values of q. For small q, however, there is a straightforward procedure to generalize Eqs. (2) and (4), to first order in q. When members of both species coincide in a given cell, the survival of either one occurs at the cost

of the other's death. The probability of such coincidences is $\chi(q)\chi'(q)$, where $\chi(q)$ and $\chi'(q)$ denote the occupancy fractions of the stronger and weaker species, respectively, when $q > 0$. Whenever one such coincidence event occurs, there is a probability q that the weaker species will win; hence to first order in q, the occupation fraction for the stronger species becomes

$$\chi(q) = \chi - q\chi\chi', \qquad (5)$$

where χ and χ' are occupation fractions for $q = 0$. Similarly, the occupation fraction of the weaker species takes the form

$$\chi'(q) = \chi' + q\chi\chi' \qquad (6)$$

The persistence condition for the weaker species,

$$\Gamma'/\Gamma > -\chi(q)/(1 - \chi(q)) \ln(1 - \chi(q)),$$

becomes, to first order in q,

$$\Gamma'/\Gamma > -\frac{\chi}{(1 - \chi)\ln(1 - \chi)} + \frac{q\chi\chi'(\chi + \ln(1 - \chi))}{[(1 - \chi)\ln(1 - \chi)]^2}. \quad (7)$$

It is straightforward to show that the second term in this inequality,

$$\frac{q\chi\chi'(\chi + \ln(1 - \chi))}{[(1 - \chi)\ln(1 - \chi)]^2},$$

is negative in the interval $0 < \chi < 1$; hence, as expected, the fertility advantage of the weaker species does not need to be as large when $q > 0$ as it is when $q = 0$, in order to coexist with the stronger one.

As an example of the use of the above formulas, we consider a situation where $q = 0.1$, with parameter values $\Gamma_1 = 400$ (stronger species), $\Gamma_2 = 2000$ (weaker species), and $H = 0.0032$ (all quantities in arbitrary units). In the limit $q = 0$, the two species coexist, with population fractions, $\chi = 0.3873$, and $\chi' = 0.5988$, respectively. To first order in $q = 0.1$, one shows that condition (7) holds, so both species are able to coexist, with population fractions $\chi(q) = 0.3615$, and $\chi'(q) = 0.6245$.

4. Discussion

We consider here the connection between Skellam's results supplemented with our extensions above, and current research on ecological niches, population dynamics and species competition.

Niches. The case of total species segregation is especially relevant from a biological point of view, through its relationship with the concept of ecological niche. In its original version (by Grinnell [8] in 1917), a niche referred to the actual physical space occupied by a given species. This notion was further elaborated by Elton [9], who located a species niche within its foodweb. In 1957 Hutchinson [10] gave the concept its most abstract definition, associating with each species a region in a multidimensional space whose axes are quantified biotic and physical attributes relevant to its survival. In

this version, a niche is an attribute of the species, instead of its habitat, as in the case of Grinnell [8], and Elton [9]. Later work [11] has developed mostly along the lines of Hutchinson's approach.

In Skellam's work, cells are physical entities, in the sense of Grinnell [8], but their suitability is quantified closer to Hutchinson's definition [10] through the fertility factor, and the probability that a seed survives to maturity in a given cell, as this probability depends at least partially on features like germination speed and nutrient storage that are intrinsic to the seed. A possible way to quantify the relationship of Skellam's cells with Grinnell's niches would be making an individual cell's size equal to the ecosystem's area divided by the population size of the species considered, under conditions of maximum productivity (*i.e.* when the ecosystem functions at its carrying capacity limit).

Population dynamics. The significance of Skellam's contribution to population dynamics in structured habitats can be judged by comparing his treatment with major contemporary lines of research on the subject. Regarding species coexistence and competition, one has models based on island biogeography [12] and metapopulation theory [4,5], and structured-habitat elaborations of the predator-prey model [13-15; see also Ref. 5, chapter 7].

Although island biogeography preceded metapopulation theory, in recent times the latter has gradually become the theoretical tool of choice in this context. In fact, island biogeography can be expressed in terms of metapopulation theory, by considering one special patch, or island (representing a continent), so much larger than the others that it remains in a steady state, regardless of the migration or death of its individuals [16; see also Ref. 5, p. 59]. Hence we deal here exclusively with metapopulation theory.

In its simplest form, it considers a composite habitat with patches amenable to occupation by various members of a given (animal or plant) species. The global population (metapopulation), is thus an aggregate of the resulting sub-populations in such patches. Each sub-population is assumed to vary in size due to migration and mortality. The first metapopulation model, introduced in 1969 by Levins [4], deals with the time evolution of the fraction of occupied patches in a landscape, $P(t)$, $dP/dt = cP(1 - P) - mP$, where c and m are coefficients of colonization and extinction, respectively. The stationary value of $P(t)$ is given by $P_{stat} = 1 - m/c$, and smaller values of P lead to a negative time derivative in the dynamical equation, hence to extinction. Habitat structure thus plays a minor role in the model, as only patch counting is involved.

Levins' model has been generalized in many ways, introducing for example individual patch abundances [17], qualifying migration according to a "rescue effect" [18,19], making colonization dependent on the distance between the patches involved [20,21], etc.

Comparison with Skellam's model of a structured habitat seems at first glance difficult, as Levins' model patches relate

to the species (hence they can be occupied by many individuals), and Skellam's cells relate to individuals. However, the mathematical analysis of metapopulations has been extended to the individual level, with minor changes [6,22].

In consonance with Levins, Skellam deals with patches in a global fashion; his patches, however, are characterized by an intrinsic quality factor (H). Levins' model, by contrast, emphasizes in and out fluxes through patch borders. In this sense, Skellam's and Levins' approaches are complementary. There is also a limiting condition for population persistence in Skellam's scheme, although it depends not on population size, but on the product of patch quality and seed production ($\Gamma H > 1$). Due to mortality, there remains in both cases a fraction of empty patches in the stationary regime.

The original treatment of species competition is the classic predator-prey model of Lotka and Volterra [23,24], where spatial structure was completely absent. Some recent models of this type do include limited space dependence [15; cf. also Ref. 5, chapter 7]. However, Skellam's method cannot be compared with the Lotka-Volterra approach in any direct way, as the former is based on an evolution condition (the recursion relation $\chi_{n+1} = 1 - \exp(-\Gamma H \chi_n)$), which involves the population fraction of a single species. When seeds or plantules from competing species coincide in a given cell in Skellam's scheme, there is no predator-prey relationship between them; species superiority is introduced by hand.

Although the matter of stability in Skellam's recursive method to study species persistence and competition in various habitats is not considered in this paper, we offer the following comments on this important question. The stability of a given arrangement of species in a uniform habitat can be determined using May's criterion for ecological stability [25], involving species richness, their connectivity and the range of connectivity "strength".

The stability of Skellam's solution for the stationary regime in his recursive equation ($\chi = 1 - \exp(-\Gamma H \chi)$) can be ascertained as follows. Let us assume that the habitat richness suffers a small change, from H to $H' = H + \delta$; the stationary regime will consequently be shifted by some amount Δ, from χ to $\chi' = \chi + \Delta$. Writing $\chi' = 1 - \exp(-\Gamma H \chi')$, one obtains to first order in δ, $\Delta = \{\Gamma \chi (1 - \chi) / [(1/\chi)(1 - \chi) \ln(1 - \chi) + 1]\} \delta$. As the coefficient of δ in this equation never blows up (it tends to Γ for χ close to 0, and to 0 for χ close to 1), we conclude that the stationary regime is stable. A similar result follows, assuming a small change in seed production, as Γ and H appear in symmetrical fashion in the stationarity condition above.

Closer in spirit to Skellam's approach are models of species competition within the metapopulation context. Consider for example Tilman's model [6], where n species compete, ranked by their competitive ability (just as in our extension of Skellam's scheme in Section II), with the first one being the best competitor, in the sense that its members outperform those from all other species, when they coincide in the same individual site. The model is based on the dynamical equation,

$$dp_i/dt = c_i p_i (1 - \sum_{j=1}^{i} p_j) - m_i p_i - \sum_{j=1}^{i-1} c_j p_i p_j,$$

where p_i is the fraction of individual sites occupied by members of species i, and c_i and m_i are the colonization and mortality coefficients for individuals from species i. This model is thus conceptually close to Skellam's proposal, and in fact, more restricted that the latter, as it involves a homogeneously rich habitat, while Skellam also deals with habitats with two sectors (a rich and a poor one), and his argument can be extended to an arbitrary number of sectors, with various levels of richness, as we did in Sec. 2. The case of partial species superiority is not considered in Levins' model.

The most relevant aspect of Skellam's work on this problem is the realization, through a mathematical argument, of a tradeoff between individual fitness and the number of offspring. A similar observation was put forward by Hutchinson in the same year as Skellam (1951) in a now classic paper [26], based on an inverse relationship between egg size and clutch size in copepods. However, the tradeoff qualitatively suggested by Hutchinson, between investment in the fitness of individual offspring, and investment in offspring number, was mathematically formalized much later [27].

Appendix

We describe here a systematic procedure for choosing sector richness values $\{H_k\}$, and seed production $\{\Gamma_i\}$, in order to have n species distributed in n habitat sectors with total segregation (*i.e.* a single species to each sector).

Let us rank the species $\{S_j\}$ according to fitness, so that an individual from S_1 survives when it confronts one from S_2 in the same individual cell, and so forth. Our problem consists in choosing values for habitat richness $\{H_k\}$, and for seed production $\{\Gamma_i\}$ (where individuals from species S_i produce Γ_i seeds), that lead to the persistence of only one species per sector. Let us start by choosing arbitrary values for $\{H_k\}$ such that $H_1 > H_2 > H_3 \ldots$; our problem then reduces to selecting the appropriate values for $\{\Gamma_i\}$.

We now associate small values of Γ with large values of H, as follows: pick Γ_1 so $\Gamma_1 H_1 > 1$, and $\Gamma_1 H_j < 1$ for $j \geq 2$. Hence the species S_1 will survive only in the first habitat. Choose now for the second species $\Gamma_2 > \Gamma_1$, so $\Gamma_2 H_2 > 1$, and $\Gamma_2 H_j < 1$ for $j \geq 3$; the species S_2 can thus survive only in the first and second sectors. Now adjust Γ_2 so that S_2 cannot survive in the first sector, so that

$$\Gamma_2 / \Gamma_1 < -\chi_1 / (1 - \chi_1) \ln(1 - \chi_1).$$

This can be done because, although we have $\Gamma_2 / \Gamma_1 > 1$, the quantity $[-\chi_1 / (1 - \chi_1) \ln(1 - \chi_1)]$ is also greater than unity (using $\chi = 1 - \exp(-\Gamma H \chi)$; one first rewrites it as

$$[\exp(\Gamma_1 H_1 \chi_1) - 1] / \Gamma_1 H_1 \chi_1,$$

and then shows that

$$f(y) = \left[\exp(\Gamma_1 H_1 y) - 1\right] / \Gamma_1 H_1 y$$

is an increasing function of y in the interval $0 < y \leq 1$, with $f(0) = 1$). For Γ_3 one now follows a similar procedure, and so forth.

Although the above algorithm involves "fine-tuning" of parameters at each step, the amount of guessing is greatly diminished relative to a random search for parameter values.

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