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Succession in stationary environments generated by interspecific differences in life-history parameters

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We propose that plant succession in environments that fluctuate randomly around some constant mean can result solely from interspecific differences in two life-history parameters, namely longevity and annual seed production. Using a model of interspecific competition for space we show that species with a high seed set and short life span are gradually replaced by species with the reverse characteristics. It also follows that species with very different life spans, but with the right combination of parameter values can coexist, as is required for a climax stage. The results show that field observations can be inadequate to distinguish between stable and unstable coexistence in ecological time.

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1. Introduction

The concept of plant succession usually refers to an immigration-extinction process that gives rise to a qualitative change in community composition over time. Many explanations for this process have been proposed (e.g. Drury & Nisbet 1973, Liljelund 1979, McIntosh 1981), but most authors agree that two of the general biological questions about plant succession are (i) why and how certain species replace each other, and (ii) why some species are "early" and some "late".

It is clear that several different mechanisms can give rise to succession. For example, gradual changes in the environment induced either by internal forces (e.g. one plant species modifying the substrate in a way favourable to another) or by external ones (e.g. land elevation giving rise to a gradually changing soil moisture regime) are known to occur in many successions. Hypotheses based on such mechanisms, then, view succession mainly as a consequence of a physico-chemical gradient in time (Connell & Slatyer 1977). The age of the habitat (i.e. time per se) exerts its influence mainly via this gradient but is otherwise of secondary importance. Accordingly, the relevant ecological parameters are primarily plant tolerances and preferences for specific physical and chemical environments. However, the temporal occurrence of environmental gradients often differs between sites, for example, land elevation causes a successively drier habitat, whereas land depression causes a successively wetter habitat. Therefore, in these cases, no general hypotheses about which species are early and which are late can be stated, only hypotheses specific to each set of environmental conditions.

In this paper we analyze the influence of time *per se* on the composition of a plant community. Consider a plant community in an environment that fluctuates randomly around some constant mean (i.e. an environment that is stationary in the statistical sense). We then propose, provided there is a triggering event that pushes the community away from its stationary state, that the following succession can be generated from two simple demographic parameters that determine the kinetics — not the tolerances — of the involved populations. These two parameters are annual seed production and longevity of the adult plant, respectively, and we demonstrate that interspecific differences in terms of these parameters are sufficient to explain differences in the rate of invasion, as well as in the ability to persist in later stages. This means that we exclude as necessary mechanisms behind succession not only systematic changes in the physical environment, but also environmental spatial heterogeneity and differences in competitive ability for any resources other than space (cf. Yodzis (1986) for a discussion of the concept of competition for space).

Other authors have addressed the same problem in different ways. For example, Horn (1976) generated a succession of tree species by using a transition matrix. His matrix elements were, however, empirically determined and not identifiable in terms of more elementary species properties. Nor did his approach include any random between-year variation in species performance. On the other hand, Shugart (1984) describes succession as species replacement in gaps following the death of a plant individual with detailed description of species properties, including biomass development. The present analysis is a compromise between these extremes in that it is based on only a very limited number of plant parameters (seed production and longevity). The theory employed belongs to the family of lottery models (e.g. Fagerström & Ågren 1979, Chesson & Warner 1981, Chesson 1982, Ågren & Fagerström 1984, Shmida & Ellner 1984), but whereas these earlier authors have focussed on the stationary properties (coexistence versus non-coexistence) the target here is time, i.e. the dynamics.

2. Theory

Consider a system consisting of a fixed number of sites, where each site can support only one adult individual. Replacement can only occur when a plant individual dies or is removed so that an empty site is made available for colonization, thus making space the crucial limiting resource. More than one seed can arrive in such a site, but only one new adult can occupy it. The recruitment of this new individual is determined through random selection (lottery) among the available seeds on the site.

We will analyze the problem of succession utilizing the model developed in detail by Ågren & Fagerström (1984). In this model, the fundamental kinetic equation for $n_i(t)$, the fraction of sites occupied by species i, is

$$n_i(t+1) = (1 - \lambda_i)n_i(t) + P_i^d(t)\, P_e(t) \quad i=1,2,\ldots \qquad (1)$$

where λ_i is the annual death rate, $P_i^d(t)$ is the conditional probability that an individual of species i will establish in a site given that it is empty, and $P_e(t)$ is the probability that a given site is empty. With this model there will always be a certain fraction of sites that are empty. Note, however, that the actual sites being empty will vary between years, namely, no sites are predetermined to stay empty (refuges).

In the general case, differential capacities of species to compete for nutrients, water and light can be accounted for by prescribing a bias in the lottery which selects the seed that will develop into an adult at a given empty site. Throughout this paper, however, we assume that no such bias exists, namely, the competitors have identical competitive abilities in the seedling stage.

Let a_i be the mean and let σ_i be the variance in annual per capita seed production of species i, and let ρ_{ij} be the corresponding cross-correlation in seed production between species i and j. It can then be shown (Ågren & Fagerström 1984) that species i can survive in the presence of species j only if the following relationship holds true:

$$\frac{a_i}{\lambda_i}\,\frac{1 + \left(\dfrac{\sigma_j}{a_j}\right)^2}{1 + \rho_{ij}\dfrac{\sigma_i}{a_i}\dfrac{\sigma_j}{a_j}} \geq \frac{a_j}{\lambda_j} \qquad (2)$$

In other words, the invasibility of i requires that its expected per capita lifetime production of seeds, multiplied by a "noise factor" which contains the stochastic elements of the system, exceeds the expected lifetime production of seeds of species j.

3. Results

In the parameter space a versus $1/\lambda$ we can for any given species i construct the hyperbola $a/\lambda = a_i/\lambda_i =$ constant, namely, an isocline of equal expected total life time production of seeds. The inequality (2)

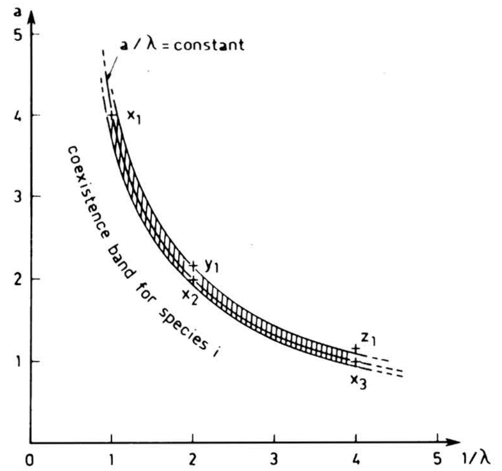

Fig. 1. The a versus $1/\lambda$ parameter space. The coexistence band for species satisfying $a/\lambda = 4$ and with $\sigma/a=0.25$ and $\rho_{ij}=0$ is shown. Species lying within this band (x_1, x_2 and x_3) can coexist. Species belonging to different bands (x_1, y_1 and z_1) cannot coexist.

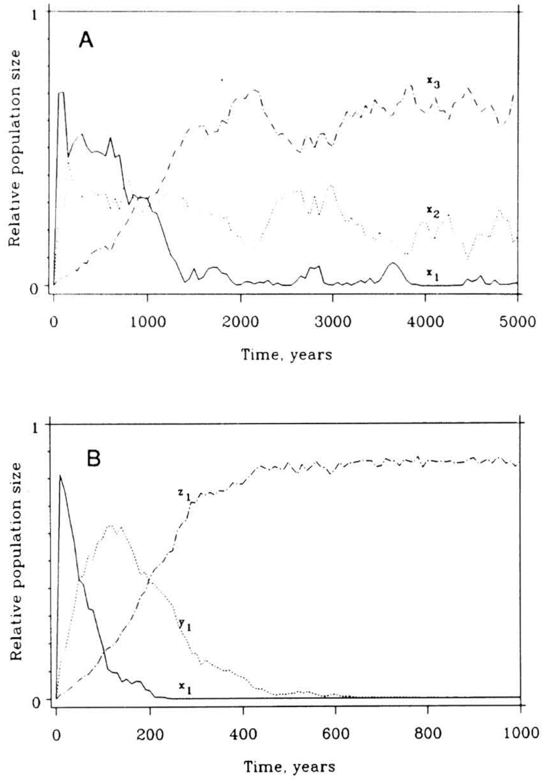

Fig. 2. The succession of species starting from low initial densities ($x_1=x_2=x_3=0.001$) and assuming log-normal distributions of per capita annual seed production. — A. The stable coexistence of three species (x_1, x_2 and x_3 in Fig. 1; parameter values: $a_1=4$, $a_2=2$, $a_3=1$, $\lambda_1=1$, $\lambda_2=0.5$, $\lambda_3=0.25$, $\sigma_1=0.8$, $\sigma_2=0.5$, $\sigma_3=0.25$, $\rho_{12}=\rho_{23}=\rho_{31}=0$). — B. A system where only one species is present in the final stage (x_1, y_1 and z_1 in Fig. 1; parameter values: $a_1=4$, $a_2=2.1$, $a_3=1.1$, all other parameters as in (a)). Note the different time scales. The species densities are the average of ten samples with a sampling interval of 50 years in A and 10 years in B.

implies that there is a band around this hyperbola containing all species j, such that species i can neither outcompete species j, nor be outcompeted by it (Fig. 1). Such a "coexistence band" connects longevity and seed set so that species with a high yearly seed set and a short life span can coexist with species with a smaller yearly seed set but longer lifespan. It also follows from (2) that the larger the variability in an environment is (expressed as σ/a), the wider the coexistence band will be and the more species there can be in the community. When two species lie outside the coexistence bands of each other (because they have sufficiently different expected total lifetime production of seeds, or because the "noise factor" is sufficiently small), the species with the largest lifetime production of seeds will eventually outcompete the other one. If we select species with overlapping coexistence bands (e.g. species x_1, x_2 and x_3 in Fig. 1), allow them to interact according to Eq. (1) and start with equal, but low, initial values, a sequence in time of increasing and decreasing abundances is produced until an equilibrium of the system is reached (Fig. 2a). Initially, species with a high yearly seed set and short life span dominate but the dominance is successively shifted towards species with a longer life span and lower seed set.

If, instead, we select species with non-overlapping bands in the order of increasing total lifetime production of seeds (e.g. species x_1, y_1 and z_1, in Fig. 1) a new kinetic pattern results. Species x_1 dominates initially but is gradually replaced by the other species until, ultimately, only the species with the highest lifetime production of seeds remains (Fig. 2b). Note, however, that the extinction can be a very slow process; in the present example Fig. 2b is qualitatively similar to Fig. 2a over the first 200 years; namely a time span much longer than the time series of species abundances accumulated in a typical field research programme. The general result emerging from these examples, then, is a consistent non-repeating change in community composition over time, namely a succession. Species with a high seed set and short life span are gradually replaced by species with the reverse characteristics. This pattern results solely from differences in these two demographic parameters; we have prescribed the species to be equal in all other respects.

4. Discussion

Our model is based on two biological assumptions about colonizing ability and interspecific competition. In the initial stage all species, even those that dominate later, are present in low abundances. This means that no typically early and late species exist, in the sense that species appearing (dominating) late need any preparation of the site to be done by those dominating early, as proposed to be the most important mechanism in the Clementsian tradition (Connell & Slatyer 1977, Peet & Christensen 1980). Instead, all arriving species have the same potential ability to become established. What we are analyzing, then, is a special case resembling the qualitative "initial floristic composition" model of secondary succession (Egler 1954).

In our model, no species necessarily has competitive superiority over any other. In some hypotheses about succession it is assumed that replacement of established individuals takes place via competition for resources, such as nutrients, water or light (tolerance model, sensu Connell & Slatyer 1977). However, there are several results from experimental studies showing that late species colonize better when early ones are absent (e.g. Keever 1950, Niering & Egler 1955, McCormick 1968, Parenti & Rice 1969), indicating that the late species need not be better competitors in this respect.

The strategies open to plant species in the current approach do not correspond to the r-K-continuum. The seed production is a measure of the intrinsic growth rate and thus similar to r. The parameter K, on the other hand, has no counterpart in our formulation because K describes the ultimate population size, which we derive as a result of the interplay between all plant properties. In addition, K is strongly coupled to the classical niche concept (i.e. resource and/or habitat segregation), whereas we idealize to a complete overlap in these dimensions. The opportunities for coexistence in our case derive from separation in the regeneration niche (Grubb 1977) in conjunction with the general feature of lottery mechanisms, namely, that randomness promotes coexistence. Neither of these dimensions are included in r-K terminology.

Fries (1853), Egler (1954), Frank (1968), Drury & Nisbet (1973), Connell & Slatyer (1977), Noble & Slatyer (1980), and Hibbs (1983) all emphasize the importance of differential longevity during plant successions, because when one plant individual occupies a site, this site is withdrawn from further establishment as long as that plant individual is alive. However, such an explanation is not sufficient. According to the present model, the annual seed set proves to be an additional parameter enabling a species to rapidly invade — and, even for a long time, to dominate — the community, even if it has a short life span. In the end, however, when the species are chosen within one coexistence band, the species with the longest life span will dominate. This is so because increases in population density are density-dependent, namely, increases depend on there being a favourable result for a given species of its interaction with the other species, whereas decreases are density-independent. Therefore, in an ensemble of species that are essentially equal competitors according to Fig. 1, species with a lower seed set and longer life span will ultimately be favoured. If species are chosen from different coexistence band it is, of course, possible to have short-lived species with very high seed production that will never let in the longer-lived species.

The empirical support for the predicted sequence of species seems in general to be good (see for example Booth 1941, Keever 1950, Rice et al. 1960, Horn 1974, Pickett 1982, Walker et al. 1986, Wood & del Moral 1987). In some real successions virtually all species persist in the community from the beginning to later stages. This corresponds to our first example (Fig. 2a) in which there are no extinctions, simply because we select our species within one coexistence band. In most real successions, however, extinction of those species dominating early will eventually take place (Fig. 2b). This observation suggests that one coexistence band does not correspond to a realistic supply of species in real communities. In general, long-lived species have such a high annual seed set that their total life time production of seeds is higher than that of the very short-lived species (Harper & White 1974). Thus, a normal constellation of species during the succession, with respect to their positions in the parameter space, should be like the one depicted in Fig. 1 for the sequence x_1, y_1, z_1. However, in the end all species must belong to the same coexistence band. Possible mechanisms of coexistence in plant species with similar niches is extensively discussed by Shmida & Ellner (1984).

The predicted correlation between annual seed set and average life span can be transformed to life-history components, namely, the resource allocation between reproductive and non-reproductive plant processes. It is generally accepted that there is a positive correlation between longevity and biomass in plants. Because of that correlation, and because long-lived species should dominate late successional stages, the total biomass, respiration and production of the whole community should generally increase during the course of succession. Our analysis thus offers an explanation, founded in population ecology, to changes in community or ecosystem parameters during successions as described, for example, by Odum (1969).

It has repeatedly been argued that since succession in the field is a complex process driven by many processes acting simultaneously, no single process can individually explain successional change and we cannot synthesize our knowledge into a unified theory (Quinn & Dunham 1983, Finegan 1984, Walker & Chapin 1987). The present analysis supports the individualistic, reductionist Gleasonian approach to plant succession; a completely dominating approach today. Yet, we agree that "Reductionism has not solved the succession problem, and will not do so while it relies on the same deduction from inadequate general models which led to the fall of the holistic scheme" (Finegan 1984). Our analysis is merely intended to focus on the only unifying aspect of all plant successions, namely, the interaction of plant populations through their life histories. It shows that a successional pattern can be explained solely from two simple population parameters — seed production and longevity — without any assumptions, for example, about environmental changes or spatial environmental heterogeneities. We do not exclude other mechanisms like environmental changes during primary successions. But — and this is important when succession theories are discussed — the present model potentially covers all types of successions. That is, during secondary successions it is reasonable to assume that the mechanism discussed above predominates from the beginning and continues to determine the kinetics of the succession throughout. During primary successions it can be assumed to start over and over again, as long as the environmental changes give rise to repeated extinction of species, on account of the environment gradually becoming intolerable to certain species.

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