

genotypes at least indirectly affect their own environment, creating closely interwoven genetic and ecological dynamics, separate analyses may be inappropriate and misleading.

Still, the notion of stable systems has a powerful attraction for research and management. This notion leads breeders to select "superior" trees by testing in "representative" environments--sites that clearly reveal "true" genotypic effects--even though production objectives and environments are anything but stable over multiple tree generations. Breeders' objectives are to increase marketable productivity, often for industrial forest management systems. These objectives and management systems often conflict with those of preservationists who seek a more naturally selected state that evolves with minimal human intervention. The notion of stability leads preservationists in a quest for fixed ecosystems with assumed natural composition, even though genetic and ecological elements are involved in a dynamic evolution that may never reach a stable equilibrium.

Thus, a conflict exists among the illusory objectives of tree breeders and conservationists. Those of us who consider ourselves to be both must re-examine the assumptions we carry about the structures and kinds of populations we breed and those we try to conserve. If both genetic and ecological systems are evolving, their joint dynamic may yield neither stable equilibria nor strong resilience to stochastic perturbations. The appropriate objective of management may not be to force a stationary state, but to manage inherent diversity. For tree breeders, this objective may require breeding for diverse populations and multiple uses. For managers of naturally regenerated forests, it may require nurturing of diverse stand structures and other factors that increase the effects of natural selection.

DENSITY DEPENDENCE

Ecology

An environmental factor that strongly affects forest health and productivity is the density of cohorts and competitors. The control of density is a prime concern of silviculturists and forest managers in planting and thinning of industrial forests and in managing gap sizes and distributions of more natural forests. Indeed, understanding the ecology of gaps may be a necessary and possibly sufficient condition for understanding forest succession (Shugart 1984). Within gaps, an ecosystem patch is assumed to exist. Depending on the number and distribution of seeds and seedlings, and on understory and overstory densities, a sequence of growth and replacement is entrained. The forest profile is then derived as the cumulative distribution of partially independent patch distributions, each with essentially the same model of gap dynamics. The dynamics of the forest profile do not necessarily lead to stable equilibria.

Such models may be only "caricatures of reality" (Horn 1981), but they are useful "in enlivening our understanding of the consequences of interactions in natural systems and in providing a tool for projecting the longer-term consequences of some of our ideas about the ways in which ecosystems

function" (Shugart 1984). In this paper, we introduce genetic variables into models of forest ecosystems. To explore joint genetic and ecological dynamics, we consider how simple density dependence can affect a single patch. We then draw some conjectures about total forest dynamics and consider some implications for management of such forested ecosystems.

Assume the simplest forms of density-dependent effects: monotonically declining fitness with increasing density, and only simple additive effects on fitness. Assume that increasing the number of individuals within a gap always decreases each individual's fitness, and that no one species or genotype has a greater depressive effect than any other. Such a simplified model would apply to an ecosystem in which pioneer species or their genotypes compete for common resources on a more or less equal footing. One biotype, however, may be able to utilize obtained resources more efficiently than other biotypes. While the envisioned system is naive, silvicultural models are often no more sophisticated, and the dynamics of even such simple systems can yield some surprising results.

Consider, for example, the dynamic complexity of an ecosystem containing only one species or genotypic component. It competes against itself and, like some pioneer species, reproduces whole evenaged stands within a patch more or less periodically. The number of individuals that can be established and reach sexual maturity per individual parent (the reproductive potential) is then only a function of the number of parents in the previous generation in that patch of the ecosystem. One might expect that density in sparsely stocked stands would increase and that in heavily stocked stands it would decrease over at most a few generations or reproductive cycles, so that an equilibrium density would be reached no matter what the initial density was. It is well known, however, that if the reproductive λ is high enough at low densities and if the trees are very sensitive to increases in density and X drops rapidly enough, the equilibrium density becomes unstable (May and Oster 1976). Then both a high and a low critical point can exist, with the population alternately bouncing between them in a cycle of period two. In fact, with a drastic enough decline of λ near the equilibrium replacement rate ($\lambda = 1$), multiple equilibria can be generated, and the population may periodically bounce among all of them, or approach a mathematically chaotic behavior.

Most genotypes and species have more complicated responses to density. Many require some shade and some minimum amount of protection against physical or biotic elements of the environment for birth, growth, and reproduction. As a result, they do not survive or reproduce well at very low density but thrive at some higher density. At very low densities, fitness is too low for self-replacement ($\lambda < 1$), but fitness rises well above the $\lambda = 1$ level and peaks at some relatively high density before ultimately declining below a self-replacement rate ($\lambda < 1$) beyond some ultimately critical density. The dynamics of such models can be even more interesting than those of pioneer types and these have been partially explored by many mathematical ecologists (e.g. May 1984).

More interesting yet for forest ecologists are the dynamics of systems when two or more species or genotypes that have different density responses

interact within the same patch. The intuitively reasonable expectation based on stable equilibrium models is that the system will move toward the equilibrium density of the genotype with highest density at which its $\lambda = 1$. This "climax" type will exclude its competitors since their replacement rates (λ 's) will be less than 1 at those densities. The ultimate competitive struggle is assumed to exist only among climax or late-successionary types at the high stand densities. The fact that these types generally have $\lambda < 1$ at low densities is assumed to be unimportant. This fact is critical, however, if under such severe environmental stresses the densities at which the of early succession or "pioneer" types, λ_p , falls below 1 are lower than the densities at which the later successionary or "climax" types, λ_c , initially rise above 1. In that case, the "pioneer" type can exclude the "climax" type if the system starts at a sufficiently low density. If density ever rises to the point where $\lambda_c > 1$, however, the "climax" type can exclude the "pioneer." Thus, at latitudinal or elevational timberlines or at the edges of arid zones, genotypes or species that might otherwise lose out or be rarely seen may form stable communities. If they are "protected," density in the community may rise sufficiently to exclude them. Hence, the protective management of particular kinds of patches can inadvertently decrease diversity. Conservation programs, therefore, may have to consider multiple management plans for a distribution of protected and unprotected patches.

If we further consider how instabilities of equilibria in one type affect competitive interactions, even of these simplest types of density dependence, many results emerge that are not intuitively obvious. Even in the competition between two "pioneer" types, it is possible for the type with a lower density tolerance (a lower density at which $\lambda = 1$) to exclude its more tolerant competitor if the density at which $\lambda_p = 1$ is an unstable point. We can also prove (Bishir and Namkoong in prep.) that if a more tolerant competitor has an unstable critical point, its instability can permit the two pioneers to coexist. If the instability of the more tolerant type is high enough for mathematical chaos to exist, it is possible that coexistence can be ensured. Thus, unstable critical points in the simplest competitive interactions of pioneer vs. pioneer type force us to reconsider our most fundamental ecological intuitions. Clearly, in the competition between pioneer and secondary succession types, or even between two or more climax types, our intuitions do not lead to confident prediction of events in any one patch or any distribution of patches. Stable equilibria of less tolerant types can reduce the chaos of more tolerant types into coexistence cycles of different periods, but chaos in one type can also lead to competitive exclusion of one or the other type or to chaotic coexistence. All of these results are rigorously derived elsewhere from the simple model described earlier (Bishir and Namkoong in prep.).

DENSITY DEPENDENCE

Genetics

Genetic variations in response to density may take different forms for germination, survival, growth, and reproduction, but for simplicity's sake, as above, we assume that a single response function approximately describes the relationship of fitness to density. If we further simplify the dynamics by

considering continuous rather than discrete reproduction, much of the complexity described above disappears. In simple models, only boundary or single interior equilibria exist, but where multiple equilibria can exist, as in the case of a pioneer type, $\lambda_p - 1$ occurs at a lower density than any climax competitor can replace itself ($\lambda_c < 1$). In all cases, however, our simplified assumptions prevent stable equilibria from being destabilized by increases in the rate of change in λ . Since the depressive competitive effects of the different genotypes on each other depend on the frequencies of genotypes, either coexistence or exclusion can ensue, even among pioneer types. Even within a single species, frequency-dependent selection can generate a variety of behaviors, including selective loss of alleles, one or more stable intermediate allele frequencies, or stable cycles of allele frequencies and population densities (Namkoong and Selgrade 1986). In interspecies competition, simple density dependence of allelic effects can generate surprising changes in directional selection (Selgrade and Namkoong 1986). With frequency dependence in linear models of competition effects, stable cycles in relative species densities and allele frequencies can exist (Selgrade and Namkoong 1985). We are just beginning investigations on fitness functions that may be more appropriate for secondary succession and climax types of genotypes, but we expect to discover additional possibilities of dynamic behavior for competition among species with genetic variation. Considering these types of interspecies effects in discrete generation dynamics opens even wider possibilities for investigating how species interact and how genetic variations in density responses can force qualitatively different ecological behaviors. Clearly, the mere existence of genetic variations does not exclusively drive the dynamics of ecosystem relationships, but neither do ecological effects at the species-ecosystem level exclusively drive allelic variations. Therefore, we can neither reduce one to the other nor understand one without the other.

With such varieties of behavior in forest genetic/ecological systems, variations in allele frequencies, genotypic and phenotypic traits, and successional states can exist for several reasons, but only some of them may be important. Whether a system has a single, globally stable equilibrium or is more complex, stochastic variations may exist among patches or gap stands that are identical in their dynamics. If the dynamic is simple, stochastic variation is merely noise, and any sampled ecosystem will be expected to ultimately go to the same stable equilibrium. With more complex dynamics, however, stochastic variation or gametic migration among patches can not only make the effects of selective forces difficult to discern, but may make diversifying selection seem to be homogenizing. There are two distinct effects that could discriminate among patches: (1) The patches may be environmentally similar but represent different starting points in the dynamic system and may be moving to different allelic and density configurations. (2) The patches may be effectively different, and their dynamics may be forcing qualitatively different system behaviors. In either case, the homogenizing effects of migration among patches can obscure diversifying selection and prevent certain states of nature from developing.

States of nature that we do not observe may be as "natural" as those that we see. For most forest tree species with their wide pollen flight, seed flight, or both, tendencies toward localized selection effects are obscured. Studies of microevolution in forest trees (Brotschol et al. 1986, Tigerstedt

1984, Roberds and Conkle 1984, Ross 1988) reveal the potential for differentiation of highly localized populations but wide pollen or seed migration at least occasionally overcomes selective propensities toward differentiation, and possibilities of local differentiation are masked. We do not know whether localized populations would generate higher levels of fitness if migration were limited, or whether breeders could develop more highly productive varieties by multiple population management.

GENETIC MANAGEMENT AND CONSERVATION

If the comforting assumptions of independently stable genetic/ecologic equilibria are logically untenable and biologically naive, we appear to be left without clear ecological and genetic objectives. Preservationists are left without a defined state toward which to aspire because any "equilibrium" is an arbitrary fixation of a dynamic system--a historic concept without much basis in biological reality. Similarly, breeders do not have a stable genetic resource base or a single "ideal" genetic composition toward which to aspire. In both cases, however, the motivations may be valid even though the biological assumptions are naive. Preservationist motivations appear to be based on values placed on at least some of the organisms themselves, independent of their utility to humans. Such values might be satisfied by an inclusiveness of biotypes and by maintaining some distribution of genotypes, populations, species, and ecosystems. For a goal of inclusiveness, the objective could be to allow natural regeneration or even selective mating to create wider variations than currently exist. For a goal of maintenance, the objective could be to maintain a finite core network of different biotypes.

The motivations of breeders are based on some ultimate utility of their breeding populations. Given the variability of available source populations and of both current and future needs, utilities of multiple populations could be roughly defined. Using the approach of some agricultural breeding organizations (e.g. Kannenberg 1983), a hierarchy of populations could be developed in which the base breeding populations would be very much like the core network of the preservationist's populations. For immediate use, populations could be selected for certain traits that maximize utility. Selection objectives for intensive breeding would be based on current utility, but there is no inherent managerial discontinuity between satisfying preservationist and breeding objectives in multiple base populations. While there is a clear dichotomy of goals, the biology of unstable systems seems to require use of multiple populations that could be substantially identical for both objectives except for how selection is used to satisfy short-term objectives.

This form of population management echoes the concepts of forest management advocated by Raup (1964) who suggested that "... it is probably reasonable to strive for efficiency in resource management only in the short run. Uncertainties in the long run call for the greatest possible flexibility in resource use. It is commonly assumed that these two objectives are incompatible, but I think we have reason to believe that they are not so in all cases." We hope that we have further enriched his concepts.

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