Biodiversity — Issues in genetics, forestry and ethics

by Gene Namkoong

The conference title asks whether we should be concerned about Biodiversity. Some would say "No". They would assert that we can engineer genes, trees, forests, and the requisite variations in them to meet future exigencies. They would assume that the biota is robust, and see forests as an intermediate stage between genetic engineering and the production of economic value. In this caricature of an extreme view, forestry can be reduced to genetic engineering, and foresters are expected to consider only the production of marketable values. The diversity that exists outside of our breeding populations is irrelevant to anything that we ought to do and ethical consideration is limited to the marketplace.

An alternative view is that all things are tightly bound into interdependent networks and that all losses of diversity adversely affect all elements of the biota. Natural systems are seen as maximally stable, diverse, and productive of all values, while human activity is necessarily destructive of this apparently fragile ecosystem. There is also an inherent good to natural systems and our only option is to preserve whatever remains that is natural. In contrast to the extreme reductionism of the "engineering" view, this extreme holism is the paradigm of nature, and ethical consideration is often extended to future generations not only of humans, but also of communities and ecosystems (Devall and Sessions 1985).

These views are poles apart in their concepts of nature, and lead to vastly different management principles. They are also dominating forest policy debates and forcing decisions either to plunder or to withdraw all management. Framed in these terms, biology is irrelevant, and forest practices are determined solely by political and legal considerations. The fact that neither engineering nor naive holism is biologically plausible does not enter the discussion. The fact that both views assume simplistic ethics without considering conflicting values is omitted from debate. Both ethics and biology are made irrelevant by naive assumptions, and uncommitted forest biologists are rarely consulted even to develop the background information on which decisions are made. Rather, major decisions on how forests are to be managed are made in legislatures and courts without much professional input from foresters. They reflect conflicting compromises that can only leave the forester vulnerable to an increasingly acrimonious battering by both sides. Forest management then becomes an *ad hoc* series of decisions that bend in the political winds; now favoring "threatened and endangered species", then increasing harvest levels; now adding wilderness preserves, then increasing road access. The latest blow to any sense of relevance that the forester may have left is now delivered by the demands for the conservation of "biodiversity".

We thus seem to be locked into a zero-sum game where what one side wins in productivity, the other side loses in ecological values and future security. Biodiversity is assumed to exist along a single dimension where an engineering end is opposed to a holistic end and foresters must find a golden mean by either flip-flopping between the extremes or by finding a mid-point between contending but irreconcilable end points.

However, biodiversity is a complex of many variables that are subject to manipulation, and forest biology is a study of different levels of variation. Hence, the reduction of biology to a single dimension should at least occasion a suspicion that a false and gross oversimplification has become the accepted paradigm. The choices that actually exist for how diversity is to be distributed and managed are neither offered nor considered. It is surprising that we have allowed ourselves to be boxed into such an untenable position. We might ask if we have been forced into this position by vociferous advocates of the extremes or if we have simply abdicated the position by our silence.

To provide alternatives for forest management, we must first clarify genetic biodiversity concepts. In particular, since genetic diversity and genetic management systems fundamentally affect stand, species, and community diversities, we must describe the status, structure, and dynamics of genetic diversity within an ecological context. Moreover, the structural and dynamic relationships between multiple levels of biotic organization need clarification. In this paper, I review three major biological factors that lead to management alternatives, and briefly discuss biologically feasible alternative management objectives. I suggest that the demands that management of biodiversity imposes on our traditional biological and forestry disciplines require a far greater integration of presently fragmented fields of research and of management techniques than previously considered. However, this integration can also reunify forestry into a cohesive field of study. I hope that this conference leads to a greater appreciation of the kinds of research and future directions that forest geneticists need to make to address these larger issues. Ultimately, our profession must also be involved in defining feasible and appropriate goals for forest management. We must, therefore, accept responsibility for developing a conservation ethic.

Diversity and Variation

Whichever of several definitions of biodiversity that we prefer to use, it is clear that biodiversity is group property, with values and characteristics that exist beyond those of any single element. At the gene level, we often speak of the variance of allele frequencies or some associated measures such as the genetic variance of a metric trait. Individual alleles at particular loci may have particular value, but variation in itself is of value to the present and future individuals, stands, and species in which it occurs. Individuals and populations are buffered, and species and communities can evolve in response to selection. All of these concepts are well known

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to geneticists and I only wish to emphasize three features of these genetic systems.

First, the role of specific alleles in response to selection is rarely clearly known. Single, qualitative gene effects are usually known only when normal physiological functions fail. While these failures give us information about developmental processes, most genes operate in complex interactions with many other effects at the transcription, cell, tissue, organ, and organism levels, within certain ecological contexts. Hence, even apparently neutral allelic variations can have selective effects that are not easily discerned at any one level of biotic organization, or at any one time in the life of an organism. Thus, variations may have values that are difficult to measure.

A second feature of genetic systems is that some alleles, individuals, and populations must decline or go to extinction and can do so while increasing some measures of variance or diversity. Extinction at one level does not necessarily decrease all levels of either diversity or value. Hence, the question is not whether losses will occur, but rather how we wish to manage losses so that some measures of good are maximized.

The third point that needs some emphasis is that diversity is usually not homogeneously distributed. Rather, significant structural components can exist that require conservation and provide opportunities for management alternatives. In ecological terms, these structures can be reflected in the difference between alpha (within population) and beta (between populations) diversities (Pielou 1975). In genetic terms, diversity is often measured by population differentiation and estimated by any of several distance statistics, or simply by the inter-provenance variance. Measures of species and community turnover rates express the same kinds of differentiation, and hierarchies of differentiation can be estimated by hierarchical measures and estimators.

The fact that hierarchies can be measured should not be taken to imply that natural structures are necessarily hierarchical. For example, if migrations between different populations or variations in population size occur, single composite measures are mixtures of heterogeneous elements of variously connected populations. If we are interested in the actual structure of variation, hierarchical statistics can only serve as useful guides to our thinking, and not as true pictures of reality.

We often use different statistics to measure different features of populations. The various F-statistics of Wright (1978), Cockerham's thetas (Cockerham and Weir 1977), Gregorius' distances (Gregorius and Roberds 1986), etc., use allele frequency differences in different forms, while the numbers of common and rare alleles are also taken to estimate features of past migrations and relatedness. Effective population size is measured for continuously distributed, island, or various other models of physical and genetic population structure. Thus, certain measures are taken to describe factors that influence population structure. At the higher levels of biotic organization, other measures provide understanding of what may be important factors that influence the viability and distribution of species, communities and landscapes. To understand the structure of nature we use many measures of diversity. To manage diversity, we must learn to manipulate several interacting factors. Therefore, diversity is not simple or one dimensional, but is subject to

manipulation. It is obviously possible to destroy whole biomes since, in one year in one country, 10 million ha. of forest were converted to a degraded, depauperate condition. On the other hand, by selecting and managing different ecosystems and increasing species and genetic differentiation, it is easy to increase beta-diversity.

Multilevel Dynamics

It is obvious to geneticists that gene frequencies change with genetics in accordance with certain rules. Population genetic research is directed to defining those rules as functions of population size, viability selection, mate selection, migration, etc. Variations in the environment over time and space are sometimes considered, but they are, at best, modeled as randomly varying factors that are not strongly influenced by genotypic variation. At the level of molecular and developmental genetics, the environment of the gene is usually considered to be fixed and effects of nuclear, cell, tissue and organic environmental variation is considered to be statistical noise. At the level of ecology, population viability and species interactions are studied assuming that genetic variations can be treated as statistical noise, that merely inhibits our ability to discern the presumed constancies of ecological interactions. While it is certainly easier for each of us to stay within the confines of our well-defined biological disciplines, we must ask ourselves if the diversity at each level of biotic organization can be treated as independent of other levels. Does genetic variation affect such phenomena as population growth and individual survival? Does population viability affect species composition? Do genotypic differences exist in their response to community composition and do they differentially affect the interactions with and of other species (Selgrade and Namkoong 1991)? Obviously, the answers to all these questions is, "Yes!". More than 40 years of growth and competition studies show that genetic variations exist in all of the factors of life history that affect growth, survival, and reproduction. Studies of resistances and susceptibilities to pathogens and pests show that significant genetic variations exist in the interactions. Beneficial effects and mutualisms among insects and trees can also affect and be affected by genetic variation. We are just now beginning to seriously study genetic variations within multiple-species plant communities, but there is no reason to expect any lack of genetic variation in at least some of those interactions. The evolutionary history of any single trait must therefore be viewed within the context of many fitness factors, including interactions with other species. The question is not whether genetic and community ecosystems interact, but which interactions are most quantitatively and qualitatively significant.

Even diffuse interactions such as chemical defenses that affect several species can have complex effects on community dynamics (Futuyma 1979). Such diffuse effects can be modeled as an average fixed effect with variance. However, such effects are often associated with frequency-dependent selection that generates qualitatively different population- or community-level dynamics. We may thus expect many interactions to be weak, but some to be strong.

Genetic effects can change community dynamics, and community composition can change genetic dynamics. Hence, the treatment of dynamics at each level of biotic organization as independent may be a convenient but misleading

falsehood. The difference in measures of diversity at different levels and the differences in the rules of transitional dynamics of genetic variation and community composition create analytical and theoretical problems. Nevertheless, the management of biodiversity requires that we consider multilevel dynamics.

Changes

The third major biological factor to discuss in the dynamics of diversity is that changes in means, variances, and differentiation are part of the nature of things that we seek to conserve. With changing global and local environments, breeders usually try to maintain and improve some measure of economic productivity while preservationists try to maintain some state of nature. To do either requires at least some minimum level of variation. However, the variation itself is seldom defined as an object of study or management. Variation is a result of changing evolutionary histories and may be a selectively important feature of species and community structure.

A major emerging research question is the extent to which variation is caused by inherently unstable and chaotic dynamics. Tropical ecosystems have long been assumed to be more stable than temperate or boreal ecosystems. If the stability of tropical ecosystems is not well established, then surely boreal systems should not be presumed to be stable. Instead of being a noise phenomenon, variation may be generated by non-random environmental and unstable deterministic processes. Furthermore, multispecies dynamics can be influenced in surprising ways by instabilities. The dynamics of one of a pair of interacting species can be forced out of a stable equilibrium by its interaction with a species that has an inherently unstable dynamic. Therefore, the existence of one destabilizing factor of population growth in one species can destabilize an ecosystem (Franke and Yakubu 1991). Such instabilities may result from natural selection. They may be an inherent feature of evolution and need not increase extinction rates. Thus, instability is not inherently bad. Stability may in fact be an unnatural phenomenon that can only be maintained with difficulty, especially when attempts are made to fix inherently unstable successional states (Selgrade and Namkoong 1991).

Since humans have already massively intervened in most ecosystems, the stabilities of present systems are unclear. We do not know whether their stability is increasing or decreasing or whether any particular state should be stabilized as an ideal. What is clear is that interventions can affect all levels of the biota as well as the structure of variation. We can increase or decrease the effective size of a population by changing the mating pattern and number of intermating parents. That is, we can increase the within-population or alpha level of diversity. We can thin on the basis of even mildly heritable traits and change genotypic distributions especially easily in forest trees. This is possible because most species produce far more offspring than necessary only for replacement. We can design removal and planting regimes to alter the birth and death rates of trees or other plant and animal components of the forest. It is also relatively easy with most forest tree species to select for form, growth, etc. and to obtain shifts in population mean performances of 20% or better in one generation. By multidirectional selection, divergence among populations can be quickly developed even if only one population is used as an original

source for breeding (Namkoong et al. 1988). If multiple and previously differentiated populations are used, then further differentiation may be generated using different alleles and loci. Hybridization can also create different allele combinations than presently exist. Finally, by breeding for different adaptabilities to climate, soil, elevation, or other environmental variables, we can develop greater variations than presently exist or may ever have existed. Thus beta-diversity can be easily increased. If care is taken to maintain large effective population sizes, the increase in beta diversity can be achieved without sacrifice of genetic alpha-diversity. It may also be possible to achieve a higher individual-tree homeostasis by selecting for some form of individual performance stability. This trait is desirable if environmental changes are large during a single rotation. Both levels of buffering are needed and both can be developed to obtain structures of variation that can serve ecological as well as economic objectives.

It is also possible to deploy variation at the species level within or between stands and communities. Species diversity can be raised by increasing the frequency of unique species among stands, and by decreasing the frequency of common species within stands. By managing at all levels, options for different products and services can be increased. The major question is not whether the structure of diversity will be changed, it is how it will be changed and how it will be directed. One management option is to withdraw all directed management, including efforts to increase diversity at all levels. Another is to choose particular species and increase their numbers and possibly even their alpha diversity. Another is to choose a particular species diversity status at the community level and attempt to fix that composition within some set of communities. The first is a wildlands option that excludes human use or interference and permits no genetic or other management. The second focuses on species of either economic value or charismatic appeal, especially those that are endangered or threatened. This option uses such statistics as minimum viable population sizes, genetic variances, or collection sizes that would ensure the inclusion of rare but potentially valuable alleles. The third option, which focuses on landscape management, may include measures of population sizes of dominant species. National policies tend to be some mixture of these management systems, but none are necessarily good nor is any one sufficient. No matter which option predominates, the level and the distribution of diversity will be affected.

Forest Management Options

I have emphasized three concepts for plants: (1) Biodiversity involves all life forms and a variety of structures that exist at multiple levels of organization. (2) The dynamics of diversity are poorly understood but involve complex interactions among individuals, species, and communities. (3) The structure of biodiversity has changed and will change according to our choice of action or inaction. From these concepts, we can immediately refute any assertion that biodiversity is a one-dimensional concept and that our only choices are to either engineer the biota or to withdraw use and management. We can also deny the feasibility of saving all alleles, all individuals, all populations, all species, or all communities. Attempts to do so are impractical and cannot develop any ideal state. Even attempts to fix one set of

elements must disrupt the dynamics at other levels of organization and function. Storing alleles, genotypes, or individuals may be useful as a sample of populations that exist at a particular time and set of places, but that set may not be optimum for either past, present, or future needs. Saving species may not save all of their useful alleles and may not save the communities or their evolutionary dynamic. Attempts to save communities may not even save the species they presently contain. Species may be lost because they depend on dynamics that occur outside of particular communities. Therefore, preserving the *status quo* or any status is neither feasible nor desirable. In fact, there can be no static paradigm since dynamic change is the behavioral paradigm. Neither the status in the year 1991, the year 1791, nor the year 1 could serve as a model even if those conditions were known.

Even though we lack a fixed objective state for which to manage, we know that diversity is necessary for the viability of the biota. For many objectives, a managed increase in diversity can be desirable. It is possible to manage for diversity through traditional methods of gene and field management. By managing the mating system, we can maximize effective population size, and by selecting for different adaptabilities and life history components, we can diversify among different populations. This kind of management is no different than multiple population breeding for different economic or environmental adaptabilities. It is merely an extension of the set of selection objectives. Industrial forestry objectives need not be excluded as major directions for breeding, but broader forestry goals must be included. Increasing diversity can serve to increase sustainability of ecological and economic services if the diversity is so managed. It can also provide a buffer against extinction caused by environmental shift. By extending simple gene management techniques with simple selection procedures within populations to more species, we can also affect the structure of genetic diversity of a broader range of forest types than only those used in industrial forestry. By thinning selectively by species, size, and age, and by planting, we can rapidly influence the structure of genetic and physical diversity. By selecting and designing reserves, we can also increase the differentiation and available diversity for future uses. Options that are immediately available to forest geneticists are: (1) to simplify breeding procedures as much as feasible (2) to diversify selection among potentially useful species and (3) to include species that may have substantial impact on the evolution of communities and of other species. Understanding the genetics of life history traits and how they affect selection and natural evolution requires that we study the genetics of developmental and physiological systems and not just height growth and volume yield. We also must study how species densities, competitions, mutualisms, and host/pathogen-predator/prey coevolutions are tightly or diffusely affected by genetic variations. Our understanding must go well beyond single species effects in intensively managed plantations. Biodiversity thus requires that we cross traditional disciplinary boundaries and that we direct studies and management to whole forests and their subsystems.

Ethics

To develop management policies concerning biodiversity requires that we try to define a biodiversity ethic. The

following brief initial attempt to develop an ethic about biodiversity represents solely the position and thoughts of the author and may not reflect the position or opinions of The Forestry Chronicle. This attempt is based on developing a rationale for managing biodiversity that is centered on human values and utility to humans. If a rationale for biodiversity conservation can be based on these narrowly defined foundations, then other rationales based on a broader foundation of obligations to non-humans would expand upon the obligations derived in this paper. In considering the ethics of biodiversity, it is crucial to distinguish between the subjects for which we manage and the objects that we manage. The subjects for which we manage possess inherent values that we try manage. The subjects for which we manage possess inherent values that we try to increase or preserve. The objects are those things that we use; they have only instrumental value. A major ethical problem is to determine which organisms have inherent values, what moral obligations are owed to them, and which can be treated strictly as instruments. Traditionally, forests have been managed to satisfy human needs and values. People were the subjects for which we managed. Increasingly, however, that value system has come into question. For example, many if not most people would agree that certain charismatic animals have inherent rights to existence. Survival of such animals has become one goal of management. From the human value perspective, if these species are only of scenic value or are good indicator species, then their survival may be an objective only to the extent that substitutes may not do as well for our purposes. If, however, we grant that certain non-human organisms have inherent value, then a further management decision depends on whether ethical obligations exist only to specific organisms or also to the species as a whole. Management to save individuals is vastly different from management for population viability, and this is different from management for species or community viability.

Our role is thus not limited only to defining what is feasible and what is biologically possible. Perhaps, biology can more deeply inform the ethical debate. While it is reasonable for foresters to hesitate where angels fear to tread, the argument can be made that the techniques of management are not value free and, hence, that we cannot separate techniques from goals. It seems obvious, for example, that the selection of the number, size, and distribution of reserves reflects values for particular segments of the biota, and the choice of charismatic species or the assignment of designations of "threatened" or "endangered" as a management factor reflects certain values. It is also obvious that, for some, any level of any extinction is inherently evil. While fraught with difficulties for the philosophically naive, foresters cannot avoid being drawn into ethical debates, and must consider the many ethical dimensions of management actions. By hesitating to enter the debate, we only accede the field to the biologically naive and find ourselves able to serve only as peripherally significant technicians in pursuit of the objectives of the uninformed.

One of the first questions we must face, therefore, is that of how to divide subjects from objects. I will not attempt to go deeply into issues of moral standing (Goodpaster 1978) but will simply assert that moral value must reside in individual beings as opposed to groups of beings. Instead of addressing the difficult question of which kinds of species

belong to the moral community, I consider whether any holistic ethic is well-founded. If, as initially asserted, diversity is a group property, and if moral value can reside only in individual beings, then diversity may be of ethical significance only as it affects individual organisms. Unless moral significance is attributable to groups or other levels of organization, then only the effects of diversity on individual values can matter.

The problem is that while distinctive group properties and group-level dynamics may exist, it is difficult to say that any group property can endow that group with morally relevant value. I cannot see that any group can have a consciousness that can claim a good of its own beyond the value that the group may have to the individuals that compose it. Obviously, it seems that below the organizational level of an individual, at the gene, tissue, organ, etc. levels, there is no organized entity that can claim an independent good of its own. At the individual level, an independent consciousness exists. It is debatable whether group awareness or other properties held at the group level can deserve moral standing. The problem for species conservationists is not that a species as a group does not have great value to us directly and indirectly, but whether the only value they have is their service to their own individuals and to us now and in the future. For species to have moral standing greater than as a collection of individual goods, it would not matter if individuals of other species have inherent moral standing. The whole species must and thus far, no compelling argument for this has been made. Therefore, while I can and do place great importance on preventing species extinctions, it is not based on the moral standing of other species as much as it is on my obligations to present and future individuals of human and some other species. There are some animals that I consider to have moral standing and whose welfare has inherent value that I must respect. But I do not assign moral standing to the herd, or pack, or species in general. It may be good for present animals and it is necessary for future animals that the rest of their species is around, but again, the value of the species is not to itself as a group, but to some individuals. At the human level, similarly, it is certainly good that other humans exist, but it does not follow that any state or other organization has rights to existence that override any vital individual rights.

For biodiversity conservation, the critical issue is whether species conservation can be evaluated on the basis of human welfare alone, or whether there are greater obligations. Similarly, are there obligations to communities that go beyond obligations to the species that exist within them, or are community values limited to human welfare or possibly to other organisms that compose the community? If we say that we do not have clear obligations to communities as such, then we are denying the validity of the Aldo Leopold approach (Leopold 1970) to conservation which says that, "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise". The importance of denying that particular philosophy is that we would otherwise be obliged to save everything since everything is considered to be of equal value and interconnected, in some ill-defined natural state. We have already concluded that this approach is biologically infeasible, and leads to management prescriptions that place no useful priorities on our actions.

This philosophy leads to exactly the kind of *ad hoc* management prescriptions that we follow if we ignore biological input into political decisions. In fact, I believe that its uncritical adoption is a major cause of our having been boxed into a zero-sum game. It is still feasible to consider conserving communities for their ecosystem services, for study, and for their potential benefit to us or other moral beings. But if we reject Leopold, we remove the inherent value of the community and we can manage communities for the good of those organisms that have moral standing. I hope that there will be debate on this point.

If we are to accept a holistic approach to ethical consideration of the conservation of species and communities, then management strategies must consider moral claims made for species or communities. We can do so only to the extent that specific properties at those levels of organization can be said to deserve such moral standing. We can therefore consider that we accord moral obligation to those beings and those entities that we can understand may have inherent value, and to the properties of those organisms that can morally affect them. Even in this case, I believe that we can develop an ordering of conservation priorities on the basis of a principle of satisfying at least minimal obligations. That is, we have clear minimal obligations to satisfying life support obligations to humans, and to other sentient organisms. To all others and to all other levels of biotic organization, there may exist obligations to their continued existence. None of these obligations, however, can override the vital interests and life support of individuals in the more obvious moral community. Thus, we have no obligation to maintaining diversity for diversity's sake. We are obliged to manage diversity for the general good of those in the moral community. Species and communities are still desirable to conserve for the sake of their services and for our appreciative understanding of life and of ourselves, and since there may be some presently unknown but other obligation to their existence, we should try to prevent extinctions. However, we do not have definable obligations to genes or to these higher, organizational levels unless there is an independent consciousness, similar capacities, or other inherent values at those levels for which we can manage. Otherwise, potential but unknown values cannot be affected by management and, hence, management can ignore them.

If it is possible that any such obligations exist, the strongest candidates would be at the species level. Obligations to populations or communities are more dubious. Managing for diversity of species, therefore, can be inherently good, but as long as relative values among species are not definable, species of direct and indirect value to humans should take precedence, and we should manage the diversity to maximize that benefit. We can, therefore, reduce or increase diversity at the other levels if necessary and make some effort to prevent at least species extinctions. To do so will still require all levels of conservation, but with ordered management priorities. Since other ethical considerations can lead to different management priorities, we owe it to ourselves to clarify at least our own ethics.

I have neglected to directly consider the many facets of how we are to ethically manage for multiple human interests, among Native Americans and immigrants, or among conservationists and loggers, or among the many interest groups. I hope that I have offered more options for how forest

managers can assuage the contentiousness of conflicts. I hope that instead of only balancing opposing views, a synthesis of interests in biodiversity can be developed. We can construct a useful biological dialectic, that integrates presently contending views. Given the high levels of uncertainty that we must consider for future welfare, we seem obliged to maximize diversity to satisfy our minimal obligations. The variation we have today is manageable and the opportunities offered by the expanded interests in the multiple ramifications of biodiversity can allow geneticists to more profoundly affect the biota than ever before. Foresters can be the synthesizers of the biodiversity dialectic.

In considering the ethical ramifications of our work, we are also forced to consider the ethical ramifications of our own lives. In fact, we are morally obliged to be as good geneticists and ethicists as we can. We are also very fortunate to be in a field that allows us an opportunity to engage many of the deeper aspects of our own existence within our work. The question of this conference, "Should we be concerned" is thus like asking if we should be concerned with breathing. We have no choice. More to the point, we are privileged to be concerned and to have an opportunity to exercise an informed concern.

References

Cockerham, C.C. and B.S. Weir. 1977. Digenic descent measures for finite populations. *Gen. Res.* 30: 121-147.
Devall, Bill and George Sessions. 1985. *Deep Ecology*. Gibbs M. Smith, Inc., Peregrine Smith Books, Salt Lake City, Utah. 267 p.

Franke, J.E. and A.A. Yakubu. 1991. Mutual exclusion versus coexistence for discrete competitive systems. *J. Math. Biol.* 30: 161-168.

Futuyma, D.J. 1979. *Evolutionary biology*. Sinauer Associates, Sunderland, Massachusetts. 565 p.

Goodpaster, K.E. 1978. On being morally considerable. *J. Philos.* 75: 308-325.

Gregorius, H.R. and J.H. Roberds. 1986. Measurement of genetical differentiation among subpopulations. *Theor. Appl. Genet.* 71: 826-834.

Leopold, Aldo. 1970. *A Sand County Almanac: With Essays on Conservation from Round River*. Ballentine Books, New York. 262 p.

Namkoong, G., H.C. Kang and J.S. Brouard. 1988. *Tree breeding: Principles and strategies*. Springer-Verlag, New York. 179 p.

Pielou, E.C. 1975. *Ecological diversity*. John Wiley & Sons, Inc. New York. 165 p.

Selgrade, James F. and Gene Namkoong. 1991. Population interactions with growth rates dependent on weighted densities. Pages 247-256 In: Busenberg, S. and Martelli, M. (Eds.) *Differential equations models in biology, epidemiology, and ecology*, Proceedings of a conference in Claremont, CA, January 13-16, 1990. Lecture Notes in Biomath #92, Springer-Verlag, Berlin, Germany.

Wright, Sewall. 1978. *Evolution and the genetics of populations*. Volume 4: Variability within and among natural populations. The University of Chicago Press, Chicago, IL. 579 p.

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