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DEMOGRAPHIC AND GENETIC MODELS IN CONSERVATION BIOLOGY: Applications and Perspectives for Tropical Rain Forest Tree Species

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ABSTRACT

We review deterministic and stochastic demographic models as well as classical population genetic models that have been applied to tropical rain forest tree species. We discuss their implications for conservation. The main conclusions of deterministic demographic models are the key importance of species' longevity in determining susceptibility of population growth rate to harvesting of individuals at different life-stages, the critical effect of patch dynamics, and the importance of density-dependent mechanisms at least for abundant species. Population viability analysis to predict extinction times of tropical rain forest tree species has only been performed for four tropical rain forest tree species using the simplest Lefkovitch matrix linear model. Results obtained are in accordance with results of simple stochastic models for nonstructured populations that have been solved analytically. Population genetic models have shown that tropical rain forest trees: (*a*) possess high levels of genetic diversity, (*b*) maintain greater proportions of genetic variation within than among populations, (*c*) are predominantly outcrossed, and (*d*) have high levels of gene flow. These results suggest that tropical tree species may not be in immediate danger of extinction from genetic factors if actual conditions are maintained. However, the impact of forest fragmentation is expected to be particularly strong for most tropical rain forest tree species due mainly to the high genetic load kept by their present population genetic structures. Recent theoretical demographic-genetic models for simple systems suggest that the fixation of new mildly detrimental mutations may be comparable in importance to environmental stochasticity, implying minimum viable populations as large as a few thousands. It is urgent to develop a model that integrates genetic

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and demographic factors, that enables evaluations of their relative importance in long-term persistence of tropical rain forest tree species.

HIGH DIVERSITY AND RARENESS OF TROPICAL RAIN FOREST TREE SPECIES: CHALLENGE AND URGENCY

Conservation of tropical forests is one of the most urgent and challenging tasks of biologists, social scientists, environmental managers, entrepreneurs, nonprofit social organizations, and public administrators (166, 169). Much has been said on the great importance of tropical forests and the many species they harbor (see 12, 17, 121–124, 135, 170, for a few examples). Alarming projections of the rates of deforestation of tropical forests and the consequent threat of a mass extinction have also been put forward in several occasions (e.g. 12, 17, 121–124, 148, 149, 169). Of all tropical forests, those referred to as lowland tropical rain forests (TRF) harbor the greatest number of species, and their destruction would have the worst and most extensive global effects (121–124, 132). In this review we concentrate on this type of forest.

Conservation analyses of natural populations consider demographic and genetic criteria (52, 87, 141a, 149). The former refer to the size of populations and their temporal change, and the latter to the genetic variation and its distribution within populations. Both criteria have been used to estimate minimum viable populations (MVP), defined according to extinction probabilities and persistence times (24, 101, 149, 157, 158). It is impossible to obtain MVP estimates applicable to all species, but they are useful reference values to analyze the relative effects of different demographic stochasticity and genetic factors; both are likely to cause detrimental population growth and fitness effects, respectively, as population size is reduced (see reviews in 87, 149, 158). Demographic models incorporate two types of stochasticity: environmental and demographic. Genetic and evolutionary models incorporate three types of factors: loss of genetic variability for adaptive evolution, random fixation of deleterious mutations or alleles by genetic drift, and inbreeding depression (e.g. 47, 70, 90).

Tropical rain forest long-term persistence depends upon conservation of trees that are the community's dominant physiognomic elements and among which there are several key species for the subsistence of many other plant and animal species (see for example 51, 168). The challenge of TRF conservation relies mainly on the high diversity and low population densities or rarity of most tree species even in protected forests (see Table 1). For example, in Los Tuxtlas forest, more than half of the tree species had less than one individual $>$ 10 cm diameter per ha; another 20% of the species had two or less individuals; and

Table 1 Number of tree species found in a 5 ha plot with different densities per ha (individuals > 10 cm stem diameter) at Los Tuxtlas tropical rain forest (México). Data from Martínez-Romas & Alvarez-Buylla 1995.

Density range (number of individuals > 10 cm stem diam.)	Canopy trees	Pioneer trees	Medium & understory trees & palms	Total	%
< 1	29	7	18	54	55.1
≤ 2	12	3	4	19	19.4
2–10	9	1	5	15	15.3
10–22	3	1	6	10	10.2
TOTAL NUMBER OF SPP	53	12	33	98	100

only 10% had more than 10 individuals per ha. This is the general situation of TRFs (75, 78, 81). These low densities may imply that to encompass MVP (see Table 3) even all available untouched TRF areas (169) may not be enough for the long-term conservation of many TRF tree species. Furthermore, different types of rarity among TRF tree species imply different genetic and demographic constraints for their conservation (see 17 for a review).

Extinction probability increases as population size decreases (see 56, 88, 158); however, the form of the function that relates extinction risk to population size is not clear (99). For example, the relative importance of demographic and genetic factors in determining extinction probabilities in natural populations is still unclear. Lande (87) stressed the priority of demographic factors, and his view has permeated the recent literature of conservation biology (24, 113). However, Lande's own research and other studies have recently shown that fixation of deleterious mutations might be particularly important even in sexual outbreeding populations. These models suggest that this genetic factor could be as important as environmental stochasticity in populations of considerable size, determining MVP in the order of several thousands and census population sizes of more than 10,000 individuals (89, 98–100).

Although such simple models are valuable rigorous analytical tools for benchmark analyses, habitat loss or degradation and ecological factors constitute the ultimate threats of species extinction. Hence population viability analyses (PVA), traditionally based mainly on stochastic demographic models and genetic considerations, should include as much ecological reality as possible for particular analyses (24, 149, 158).

In this paper we review the demographic and genetic models that have been developed or applied to TRF tree species. These are only starting points of rigorous population viability analyses of TRF tree species. At the beginning of each section we summarize the general mathematical models or theory relevant in each case, and then we describe their applications, developments, or potentialities for TRF tree species. We pay special attention to studies of two model systems for which abundant demographic and genetic data have been accumulated: *Cecropia obtusifolia*, a light-demanding, short-lived, pioneer tree, and *Astrocaryum mexicanum*, a shade-tolerant, long-lived palm species. These are also typical species of the extremes of a continuum of life-history types of TRF tree species (8, 105). We contend that further theoretical developments that help identify critical parameters and rigorous empirical estimates of these should be urgently pursued for TRF tree species or for model experimental plant systems. PVA should consider alternative scenarios of the dynamics of the whole community's species diversity (37, 77).

DEMOGRAPHIC-ECOLOGICAL MODELS

Simple demographic models of exponential growth rate can be used as analytical benchmarks to compare predictions of more complicated models that include ecological factors such as habitat heterogeneity, succession, density-dependence, and environmental and demographic stochasticity. In this section we sequentially analyze results of models incorporating these factors for TRF tree species. We then review their conservation implications.

Lefkovitch Linear Matrix Models

GENERAL THEORY Population models applied to TRF tree species should explicitly consider demographic differences among individuals belonging to different age, size, or stage categories. Age or size structure per se may have significant effects on population trajectories (92). Caswell (29) provides a complete review of Leslie and Lefkovitch matrix models for individuals distinguished by age or growth stage, respectively; the latter is the most appropriate for plants. The general matrix model is $\mathbf{N}_{t+1} = \mathbf{P} \cdot \mathbf{N}_t$, where **N** represents the population state vector, whose elements are the numbers of individuals in a particular stage category, and **P** is a square non-negative matrix of vital rates. For large t, the proportions of individuals in different stages will become constant, and the population will grow exponentially at a constant finite rate, λ, which is the largest positive eigenvalue of **P**. Therefore, $\lambda < 1$ implies the population's exponential decrease to extinction. From these models it is possible to derive sensitivities and elasticities of λ with respect to any of the matrix entries. Elasticities are recommended because they measure relative sensitivity (i.e. they avoid the problem of comparing measurements on different scales) (39) and can be compared across populations and species.

APPLICATIONS TO TRF TREE SPECIES A Lefkovitch model was first applied to demographic estimates of *Pentaclethra macroloba* (67, 68) and *Stryphnodendron* *excelsum* (67), both primary long-lived canopy species found at La Selva, Costa Rica. Later, the model was applied to other TRF tree species (2, 3, 28, 43, 48, 67, 68, 109a, 128x, 131, 133, 134, 137; Table 1): seven understory long-lived palms, six canopy long-lived trees, and one pioneer short-lived tree. Although confidence limits of λ have been obtained only in three cases (3, 109a, 128, 131), previous simulations (10, 11) suggest that all λ's are not significantly different from 1, and hence, according to this model, most TRF tree populations would be close to a numerical equilibrium.

For long-lived TRF tree species, the largest elasticities are found for probabilities of remaining in the same life-stage (i.e. survival) during preadult and adult stages for long-lived palms and canopy tree species (see Table 2). Elasticities of λ with respect to survivorship of younger life-stages (seeds, seedlings, and juveniles), fecundities, and probabilities of transition from one stage to another (growth) are much smaller. In contrast, the short-lived pioneer tree *Cecropia obtusifolia* had greatest elasticities of λ for the transitions from seedlings to juveniles and for fecundity. These trends have been observed in other types of organisms (24).

Table 2 Estimates of population finite growth rates (λ) obtained for TRF tree species using a matrix Lefkovitch model.

Species	Life-history	λ	Largest elasticity	Longevity (yr)	Reference
TREES:					
[+]*Araucaria hunsteinii*	canopy-slow	0.9889–1.0884	Pij-a	100	(48)
[+]*Araucaria cunninghamii*	canopy-slow	1.0115–1.0202	Pij-a	100	(48)
Cecropia obtusifolia[ψ]	pioneer	0.9928–1.0346[*]	Pij-s, Gij-j, Fij	35	(11)
Brosimum alicastrum[ψ]	canopy-fast	1.0635	Pij-a	120	(134)
[+]*Pentaclethra macroloba*[ψ]	canopy-slow	1.0021	Pij-pa	150	(67, 68)
Omphalea oleifera	canopy-medium	1.0085	Pij-a	140	(133)
Stryphnodendron excelsum	canopy-slow	1.0471	Pij-pa	150	(67)
PALMS:					
[+]*Astrocaryum mexicanum*[ψ]	understory-slow	0.9890–1.0120	Pij-a	125	(137)
Chamaedorea tepejilote	understory-slow	0.9699–1.1232	Pij-pa	60	(131)
Podococus barterii	understory-slow	1.0125	Pij-pa	75	(28)
Pseudophoenix sargentii	understory-slow	1.0080–1.1995	Pij-pa	80	(43)
Thrinax radiata	understory-slow	0.9890–1.0120	Pij-pa	120	(128)
Coccothrinax readii	understory-slow	1.0129–1.0969[*]	Pij-pa	> 145	(128)

[+] Species included in Menges MVP study (111).

[ψ] Species with genetic and demographic data, see references in text.

[*] These ranges correspond to 95% confidence limits estimated according to Alvarez-Buylla and Slatkin (10, 11).

Largest elasticities found for: Pij-probabilities of remaining in the same stage (survival); Gij-probabilities of advancing to following stages (growth) and Fij-fecundities or seedling recruitment. Life-stages: s-seeds, sd-seedlings, j-juveniles, pa-preadults, a-adults.

Longevities are only approximations.

The use of the relationship between species, life-histories, and aggregate elasticities of vital rates has been proposed as an attractive and suggestive shortcut for management and life-history evolution analysis (146, 147). Important mathematical constraints exist on the elasticities of linear transition matrices, and these must be considered when making biological interpretations from elasticity analysis (52a). Structural errors in the specification of the matrix model may distort the elasticities by artificially altering the mathematical restrictions imposed on them. The sign and magnitude of these biases for such structural errors are yet to be formally analyzed.

Abundant ecological data suggest that linear matrix models are structurally incorrect for most organisms under natural conditions (24). For example, it is difficult to match the assumption of constant, density-independent vital rates with the fact that all TRF tree species have λ's very close to 1 (Table 2). Rather, density-dependent mechanisms may be affecting vital rates and limiting population growth. It is also unlikely that λ is not sensitive in the long term to environmental changes. Most TRF tree species are affected, for example, by the dynamics of gap formation and closure (see below) that varies in time and space (102–104). Detailed field work on plant vital rates and the factors that make them vary are, therefore, indispensable for an adequate specification of demographic-ecological models and for estimation of the parameters included in them.

Metapopulation Models

GENERAL THEORY A metapopulation may be defined as an assemblage of local populations that grow, become extinct, or evolve more or less independently, but are connected by dispersion. Metapopulation models, first formalized by Levins (95), have generated increasing interest among theoretical and field ecologists and managers. Most plant (82) and animal (64) populations grow and evolve either in natural heterogeneous environments or in fragmented habitats due to human perturbation. Therefore, local populations are segregated in patches of different sizes and qualities; landscape level processes as well as local conditions affect their demography and genetics. Metapopulation models may be used also to draw recommendations about how landscapes should be modified and managed to maintain or enhance biodiversity (64, 166).

Metapopulation analysis focuses on the balance between extinction and recolonization in patchy environments (69, 95). We distinguish two types of metapopulation models. The first includes simple stochastic models incorporating either constant recolonization and extinction rates or isolation-dependent recolonization rates and patch-area–dependent extinction rates (64). In these models, recolonization and extinction rates do not depend on patch state, which is usually defined by presence or absence of the species under analysis (occupancy). In this case, it is assumed that within-patch change and equilibrium occur instantaneously, in a static environment subdivided in many similar and uniformly distributed patches. At equilibrium, the metapopulation is described as a shifting mosaic of occupied and unoccupied patches, although below a threshold number of available patches, the metapopulation goes extinct because the rate of colonization is lower than the rate of extinction (64).

More recent models assume rates of colonization and extinction to depend on patch state (69, 112). The environment is assumed to be either static or dynamic (64). In the latter, the environment is a shifting mosaic of different successional stages, where in any one place the right kind of habitat is present only for a limited period of time. Thus, local extinctions are inevitable, but a species may survive in the environment if it is able to establish new local populations elsewhere, where the right kind of habitat has appeared. This metapopulation approach generally considers local population dynamics and dispersal among patches in an environmental shifting mosaic (5, 6, 72, review in 82). An interesting case developed for TRF tree populations occurs when processes at different scales have coupled dynamics. For example, patch successional stages and demographic conditions of particular local populations may be correlated (3, 5).

APPLICATIONS TO TRF TREE SPECIES Tropical forests are shifting mosaics of patches at different successional stages (25, 26, 76, 168). The forest canopy is recurrently disrupted by branches snapping or trees falling (25, 36, 106). Canopy gaps enable more direct light to reach the understory, and the humidity, soil, nutrient conditions, and biotic interactions in gaps contrast with those in closed forest (13, 25, 33, 42, 108, 140, 142–144, 164). Microclimatic conditions of gaps depend on their size and origin (33). Gaps are closed by lateral crown expansion of neighboring trees, sprouting of surviving falling trees, growth of seedlings and saplings established before the gap aperture, and by growth of newly established seedlings (36). Four main patch states (environmentally different forest patches) are distinguished (168): 1. recently formed gaps (<1 yr since opened) that may be small (ca. <100 m^2) or 2. large (>100 m^2), 3. building or successional patches (2–35 yr since opened) dominated by pioneer tree species, and 4. mature patches (e.g. >35 yr since formed) where mainly mature long-lived trees grow (106, 168).

TRF tree populations are segregated among the different forest regeneration patches. Recruitment of some species is highly dependent on gap occurrence and cohorts of different life-cycle stages are found in patches of different successional stages (3, 5). Many species recruit individuals and grow across all the regeneration mosaic; cohorts of different ages are mixed within each patch-type (107). The role of forest patch dynamics in the ecology and evolution of TRF plants has been reviewed extensively elsewhere (40, 102, 107).

Metapopulation models in TRF mosaics consider population dynamics within each patch-type, transition probabilities among patch-types determined by rate of gap formation and closure, and dispersal among patch-types (5). Patch-specific population dynamics is modeled with matrix models as described above. Within-patch dynamics has been coupled to forest dynamics by assuming that the latter is independent of the dynamics of any particular species. This is reasonable in species-rich TRF (3). A finite linear Markovian process has been assumed to model forest dynamics as: $f(t+1) = \mathrm{D} \cdot f(t)$, where D is the forest matrix with entries d^{kl} representing the constant probabilities that a patch-type l becomes type k from t to $t+1$ and f is a vector of the number of patches, if all patches are assumed to be of equal size (72), or a proportion of area of each patch-type, if patches are allowed to vary in size (3, 5).

Overall metapopulation dynamics is modeled as $n(t+1) = \mathrm{G}\ n(t)$, where G is a matrix of all possible transitions ($g_{ij}^{kl} = p_{ij}\ d^{kl}$) among life-stages ($ij$) and patch-types ($kl$); and the vectors $n(t+1)$ and $n(t)$ contain number of individuals (n_i^k) in each life-stage (i) and patch-type (k) at time $t+1$ and t, respectively. Therefore, the dimension of a metapopulation matrix would be equal to the number of patch-types times the number of life-stages. If it incorporates regeneration dynamics, it has entries in all submatrices for which valid transitions among patch-types were defined in the Markov matrix D. Along the main diagonal of matrix G are patch-specific, population-dynamics submatrices. A metapopulation matrix with zeros in all but these submatrices would model environmental heterogeneity but no regeneration or successional dynamics. Finally, seed dispersal among patch-types has been explicitly considered (3, 5).

A two-patch model to simulate *A. mexicanum* metapopulation dynamics, at Los Tuxtlas, showed that the chance of λ being smaller than 1 only increased with significant increases in gap size and fast forest turnover rates (108). This is explained by the fact that only in large gaps are the adults' survival rates reduced, and in this species, λ is most sensitive to changes in this transition (see Table 2). In contrast, for the pioneer tree *C. obtusifolia*, colonization but not extinction was affected by large-gap formation in the same forest (3). The λ estimated with this model was significantly larger than that obtained when the environment was assumed to be homogeneous and constant (see Table 2), because in stable-stage conditions, the area occupied by building patches (where mature *C. obtusifolia* grow) would be greater than that found in present conditions. Analytical and simulation analyses of this model have shown that the response of λ to changes in different entries of the patch-dynamics matrix (d^{kl}'s above) are not intuitively obvious even in a species with such a tight dependence on gaps for regeneration as this one (3). Such nonintuitive results highlight the importance of formal models to guide analyses of the effects of different disturbance regimes on TRF tree species dynamics.

Similar generalized Lefkovitch models with immigration were used to predict seed densities in different patch-types and to quantify the relative contribution of seeds from different sources to seedling recruitment (5). For constant seed rains, an analytical solution of the equilibrium number of seeds per patch-type was provided. For seed rain modeled as a function of forest patch structure, simulation results were presented. These models were validated because the equilibrium seed densities per patch-type they predicted were very similar to field estimates independently obtained from soil seed samples (5, 7). More than 90% of the yearly recruited seedlings in a 5-ha plot originated from seeds < 1 year-old (seed-rain). Analytical solutions of both models (ER Alvarez-Buylla, R García-Barrios, in preparation) yield general results and these models may be used to estimate seed densities per patch-type and number of years to attain equilibrium densities for any species.

Besides being prone to patch dynamics within natural forests, TRF tree species are also expected to have metapopulation structures at the regional level that result from the fragmentation of the forest, caused, for example, by human deforestation. Metapopulation models developed for TRF tree species have only considered gap dynamics (5), corresponding to metapopulation models of the second type described above. This is a shortcoming if gap dynamics in a particular fragment depends on regional metapopulation dynamics.

Nonlinear Models: Density-Dependence

GENERAL THEORY Density-independent factors may cause fluctuations in population size, but they are not related to the population's density or growth rate, which determine the pattern of temporal fluctuations of population size in density-dependent models. These models consider demographic rates to be functions of density, instead of constant, and in them an equilibrium population density (K) is attained (21). Accurate empirical estimates of these models' parameters are particularly important because, depending on the values of these parameters, complex dynamics may be predicted (109). Despite this fact, and that density-dependent resource limitation is expected even in some rare species (24), rather few examples of empirically parameterized density-dependent models are available for plants (145). Density-dependence is also age and/or size-dependent (156), and including these factors in matrix models makes analytical solutions difficult to derive.

APPLICATIONS TO TRF TREE SPECIES Several empirical studies have evaluated the negative effect of density on seed and seedling survival (7, 35, 142, 143), on juveniles's growth and survival (37), and on adults' growth, survival, and fecundity (49, 55, 74) for several TRF tree species. However, overall population dynamics models may be developed for only a few of these species for which complete life-cycle information is available (3, 37, 49, 74).

Some authors have suggested that density-dependent effects are significant only among high-density TRF tree species (37, 74). Data collected for tree species at Barro Colorado Island tropical rain forest suggest that very few tree species have density values at or near carrying capacities, where density-dependent regulation could be important. Density-dependent effects have been detected only in the abundant canopy tree *Trichilia tuberculata* (37). These results suggest that most tree populations fluctuate due to density-independent factors. Detailed field and model analyses for *C. obtusifolia* and *A. mexicanum*, at Los Tuxtlas, suggest that density-dependent factors may be important in the population dynamics of these species (3; M Martínez-Ramos, in preparation). Both are among the most abundant of their type (see Table 1), but the first has a very patchy distribution, and density effects were evaluated locally (37, 74).

Field evidence of density effects on survivorship and fecundity of females $>$ 20 cm diameter were incorporated into *C. obtusifolia*'s matrix models with and without patch dynamics. A negative exponential function and an increasing linear function were adjusted for fecundity and mortality, respectively. This model was analyzed with simulations. Without patch dynamics, a stable population was reached, and numbers of all life-stages leveled off at a total population size (K) very similar to that observed in the field. This model predicted a population structure that was not statistically different to that in the field. With patch dynamics and seed dispersal, the number of individuals per life-stage and per patch-type attained equilibrium values more than twice those in the field. This suggests that gap availability varies with time (i.e. in some years no adequate gaps are available for this species, and thus population size fluctuates below K) (3).

The inability of seed predators to detect seeds when these are not clumped determines that in *A. mexicanum* the probability of seed removal increases with seed density and the transition probability from seed to seedling stage decreases (139; J. Sarukhán et al unpublished). Also, juvenile survivorship decreases as juvenile density increases; no other density-dependent effects have been detected at other life-stages (49, 108). These effects were introduced into a Lefkovitch matrix by making relevant matrix entries linear functions of density. The model predicted a value of K six times larger than the observed density in the forest (M Martínez Ramos, unpublished data). According to these results, the present population at Los Tuxtlas should be increasing and long-term data have actually shown population increase (J Sarukhán and collaborators; 49).

Perhaps severe adult mortality events caused by climatological events (hurricanes) keep the population below its carrying capacity and growing (i.e. $\lambda > 1$).

Relative Effects of Different Factors

When one projects the population dynamics of a species with a particular model that has been parameterized with field data, it is difficult to know if it incorporates the key factors affecting the population. This is the approach that most tropical and nontropical applications of population models have followed (but see 22 and 156). An alternative approach is to map the contrasting results of population growth rate (in density-independent models), total size (carrying capacity population size in density-dependent models), and population structure, obtained when applying different models, to the assumptions of the models (3). This approach was used to quantify the isolated and combined effect of two factors affecting population change and structure in TRF: density-dependent demographic rates and density-independent environmental change caused by patch dynamics (3).

This approach was used for analyses of four models discussed in the preceding sections for *C. obtusifolia*. Model 1 was a simple Lefkovitch model that did not incorporate density-dependence or patch dynamics. Model 2 added only density dependence; model 3 added only patch dynamics. Finally, model 4 combined both. The dependence that this species has on gaps, as documented by extensive field data (7, 8), may be evaluated theoretically by comparing finite population growth rates and structures predicted by the linear models 1 and 3, or by comparing the population growth rates at particular times and the carrying capacities predicted by density-dependent models 2 and 4. We proceeded in a similar way to evaluate the role of density-dependence (i.e. we compared model 1 vs model 2, and model 3 vs model 4). While patch-dynamics significantly affects population growth rate and size, density-dependence regulates growth and significantly affects population structure (3).

This approach yielded general theoretical considerations as well. For example, for species that actually grow in heterogeneous environments, assuming a homogeneous environment in the population dynamics model may obscure or exaggerate the regulating effects of density-dependent factors (see also 65). For example, horizontal field studies may detect prolonged positive growth rates (i.e. those obtained in model 4 when $N < K$), and these may be erroneously interpreted as slow density-independent growth in a static environment. This might be the case of the observations made, for example, for the *A. mexicanum* populations (see above). This erroneous interpretation is due to a misspecification of the model (structural errors of the model) (cf 24), and it may yield an erroneous evaluation of the effect of density-dependent mechanisms with respect to density-independent ones on population dynamics (3).

When density-dependent mechanisms are detected (see e.g. in 74), their effect may be evaluated erroneously if patch dynamics are not considered. If patch dynamics affect population dynamics, the effect of density-dependence should be evaluated by comparing results of a model 4 with those yielded by a model 3. However, when patch dynamics are not considered, the comparison is actually between a type 2 model and a type 1 model (see e.g. 74). Erroneous evaluations of density-dependent effects due to misspecifications of the true model underlying the data may be quantified by comparing the areas (A_{12} and A_{34}) between the curves of the constant functions with respect to N (λ vs N/K) of growth rates of models 1 or 3, and the power growth rate functions with respect to N ([dN/t]/N vs N/K) of models 2 and 4, respectively. For *C. obtusifolia,* the effect of density-dependence would have been underestimated 13 times if models 1 and 2 had been compared, instead of models 3 and 4 ($A_{12}/A_{34} = 1/13$). In this case, the environmental change that results when applying model 3 (i.e. increase in gap area) in comparison to model 1, causes an increase in *C. obtusifolia*'s growth rate. This explains why, if environmental heterogeneity is not considered, the effect of density-dependence is underestimated. In contrast, if we modeled the dynamics of a shade-tolerant species (*Astrocaryum mexicanum*), the same environmental change predicted by our model 3 would cause a decrease in the species population growth rate. Likewise, if models 1 and 2 (no environmental heterogeneity) were compared instead of models 3 and 4, the effect of density-dependence would be overestimated. If environmental heterogeneity and density-dependence are suspected to affect a species population dynamics under natural conditions, a model that incorporates both of these factors should be used to project evolutionary dynamics and harvesting regimes (3).

Stochastic Models: Demographic and Environmental Factors

GENERAL THEORY All population models reviewed up to here assume deterministic factors and yield deterministic predictions of constant population growth rates and stable-stage distributions (linear models), or of population size at equilibrium (K) and population structure (nonlinear, density-dependent models). However, processes affecting population dynamics operate in a stochastic fashion and yield stochastic behavior of population growth rate, population size, and carrying capacity. Therefore, both demographic parameters and outputs of population dynamics should be treated as random variables, and deterministic models should be used only as heuristic tools. Furthermore, stochastic models may yield unexpected results because of large variances, nonlinearities, or skewed probability distributions, and only these types of models may be used to generate probability distributions of times to extinction (24).

There are three sources of stochasticity in demographic-ecological dynamics and the estimation of its parameters: sampling, demographic, and environmental. Estimates of population growth rates are subject to sampling and experimental errors because they are obtained from experimental and census data on the survival, growth, and fecundity rates (i.e. vital rates or life-table parameters) of a sample of individuals. For example, if the demographic rates are estimated repeatedly from different random samples of only 10 individuals, the survivorship and fecundity estimates will vary from sample to sample in a random fashion even if the population is of infinite size and has constant vital rates. Assignment of confidence limits to deterministic and probabilistic outputs of population models is rarely performed but are indispensable (9–11, 24, 29, 160). For example, in two of three studies that we reviewed, conclusions contrasting to those reached by the original papers were suggested when confidence limits were assigned to estimates of population growth rates (11).

Uncertainty due to sampling should be clearly distinguished from the effects of random variability of life-table parameters arising from the chance realization of individual probabilities of death and reproduction. In this case, vital rates will be random variables that will fluctuate independently of sampling errors and will affect the probability of extinction of the whole population (88). Uncorrelated fluctuations across individuals give rise to demographic stochasticity, whereas perfectly positively correlated fluctuations (within each age or stage class) generate environmental stochasticity. Hence, the variance of the mean growth rate under demographic stochasticity will decrease with population size but will remain constant under environmental stochasticity. Extinction may also be due to random catastrophies, defined as large environmental perturbations that produce sudden major reductions in population size without affecting vital rates other than mortalities (review in 24).

Environmental and demographic stochasticity may be thought of as extremes along a continuum of correlations among individual vital rates. This perspective has not received attention in the theoretical literature, perhaps due to the analytical difficulties it implies, but it may help clarify the underlying causes of different forms of stochasticity (149). Environmental stochasticity may be assumed to represent a limited number of small or moderate perturbations that similarly affect the vital rates of all individuals (88), while demographic stochasticity may correspond to the effect of a relatively large number of simultaneous, uncorrelated environmental perturbations, each one affecting a very small proportion of the population (“demographic accidents”). More interesting is that demographic stochasticity may also correspond to the statistical effect of the uncorrelated responses to a single environmental perturbation of a relatively large number of different phenotypes in the population. Hence, individuals’ responses to fluctuating external factors (i.e. environmental stochasticity) are expected to be more correlated in populations with simpler age-structure, lower genetic variability, or more homogeneous microenvironments than in populations with greater among-individual heterogeneity.

Single-species stochastic models have been extensively reviewed elsewhere (see for example, 24, 163). Ecologically meaningful stochastic models are generally analytically intractable and are explored through simulation (24). However, Lande (88) has recently proposed a useful analytical approach to evaluate the relative effect of demographic and environmental stochasticity and random catastrophes on the expected time to extinction of a population without age structure and a constant per capita growth rate (r), except at the carrying capacity, K, where growth ceases. This approach also enables the evaluation of the relative role of genetic and demographic factors in population risks to extinction.

In Lande's model (88), with demographic stochasticity, average time to extinction increases in proportion to $\exp [aK]/K$, where $a = 2r^*/V_i$, and r^* and V_i are, respectively, the mean Malthusian fitness and its variance among individuals. Under environmental stochasticity, the average extinction time is asymptotically proportional to K^c, where $c = 2r^*/V_e - 1$, and r^* and V_e are respectively the mean and environmental variance of r. Contrary to Goodman (56), expected time to extinction may scale greater than linearly with carrying capacity if $c > 1$, or equivalently, if $r^* > V_e$. Therefore, expected persistence time under environmental stochasticity may be extremely long, even for populations of modest size. However, it will increase as K increases more slowly than under demographic stochasticity, regardless of the constants of proportionality or the values of $\boldsymbol{a}$ and $\boldsymbol{c}$. Finally, under random catastrophes, average time to extinction is also a potential function of K that may scale greater than linearly if r greatly exceeds the catastrophe rate multiplied by the catastrophe size. The similarity of scaling laws for extinction risks under environmental stochasticity and random catastrophes makes intuitive sense because these constitute extreme manifestations of a fluctuating environment.

APPLICATIONS TO TRF TREE SPECIES Only one example of stochastic population modeling is available for four tropical rain forest tree species (see Table 2). Menges (111) based his simulations on Lefkovitch matrices to analyze impacts of environmental and demographic stochasticity on the average time to extinction. Environmental stochasticity was modeled by allowing population model matrix entries to vary independently from year to year. To model demographic stochasticity, the same matrix was used each year but appropriate transition probabilities were applied to each individual in the population. The results were similar to those predicted by Lande for non-structured populations. Environmental stochasticity had comparatively larger effects than demographic stochasticity on the extinction risks (i.e. larger MVP were necessary if environmental stochasticity was included). Also, larger environmental stochasticity slowed average population growth, produced greater fluctuations, reduced average time to extinction, and increased extinction probability. With highest λ, extinction never occurred unless environmentally induced variation in demographic parameters was high.

In the analysis of the effects of environmental stochasticity, some demographic stochasticity was allowed due to the uncorrelated variation in the vital rates of different plant-stages. Demographic stochasticity had minor effects relative to the deterministic case, and these effects were only felt at very low population sizes. However, it represented a threat to extinction for species with low population density and λ near 1, which includes the four TRF tree species considered. One important limitation of this study is that no correlations of environmentally produced fluctuations of matrix entries were allowed (i.e. they were assumed to be independent from each other). Menges found that increasing the number of independent vital rates buffered populations against random mortality or reproduction failure. To the extent that vital rates may be relatively uncorrelated in structured populations, as Menge's study assumed, this may represent a legitimate biological phenomenon. However, correlations are likely to occur in natural conditions to different degrees depending on the biology of the species (111). Effects of such correlations on the variability of λ may be investigated by means of simulations and their comparison to an analytical approximation, originally developed to study the effect of different correlation matrices of error estimates of matrix entries for a wide range of population life-history structures (9–11). The main result is that the variance of λ is a monotonically increasing function of correlation. The role of stochasticity in TRF tree species with different life-histories and including density-dependence and patch dynamics remains to be explored.

Applications of Demographic Models to Conservation

Some of the demographic models developed for TRF have made explicit management and conservation considerations (3, 5, 128, 134, 136, 165). Most are straightforward extensions of the linear Lefkovitch model (94, 167). In a deterministic demographic model of sustainable management, the objective would be to find the harvesting conditions that maintained λ equal to or greater than one. The sensitivities and elasticities of λ may be used directly to make inferences about the consequences of altering different matrix entries (145). But harvesting regimes may also be simulated by explicitly testing the effect of removing different numbers of individuals of each stage-category (see review in 104, 134, 136), or more elaborate harvesting regimes (130). Analyses of these simple models suggest that long-lived species are very sensitive to adult harvesting, but seeds, seedlings, and juveniles or parts of adults may be extracted in considerable numbers without altering their populations. In contrast, short-lived species (ca. < 50 yr) could be heavily logged if recruitment of young individuals could be ensured. These models may provide useful guidelines, but we must keep in mind that they have unrealistic assumptions.

Environmental heterogeneity, density-dependence, and stochasticity likely mediate the effect of different harvesting regimes. In the case of linear patch dynamics models, sensitivity and elasticity analyses could also be used to infer effects of harvesting regimes. Such analyses suggest that forest patches that have not been disturbed during the last 35 yr should be set aside, and management should be performed in building patches (less than 35 years since the last disturbance) (5); contrasting results are obtained for long-lived species (104). Harvesting regimes assuming nonlinearities have been analyzed only with simulations (3). Results vary depending on whether harvesting and gap formation are coupled. In the former case, *C. obtusifolia* attains maximum carrying capacity under moderate levels of adult removal. Stochastic patch dynamics has been considered also, and by linking it to replacement probabilities of tree species with different light requirements (T Vázquez, ER Alvarez-Buylla, M Martínez-Ramos, in preparation), the effect of different disturbance regimes on the relative abundance of species has been investigated. Finally, explicit consideration of the effect of varying spatial fragmentation showed that deforestation of a wide area would decrease the potential for regeneration significantly more than if the same deforestation rate (total area opened per year) was performed by opening areas encapsuled in a matrix of undisturbed forest (5).

GENETIC MODELS

Conservation genetics estimates minimum viable populations by combining models of population genetics with estimates of rates at which different mutations arise (Table 3 and references therein). Until the early 1990s, estimates emphasized only two types of genetic effects on extinction risks of small populations: inbreeding depression (1-MVP in Table 3), caused mainly by segregation of partially recessive lethal alleles, and the loss of potentially adaptive variation in quantitative characters due to genetic drift (1-MVP and 3-MVP in Table 3) (reviews in 14, 47, 53, 70, 86). More recent models incorporate the effect of new mildly detrimental mutations that accumulate and might become fixed by random genetic drift and gradually decreasing fitness (4-MVP) (89, 90, 98–100). These models suggest that this factor may pose a serious risk of extinction in small populations.

MVP estimates summarized in Table 3, have been obtained only as reference values, rather than as definite recommendations (91), and they guide our discussion on the conservation implications of the estimators that have been published for TRF tree species. The first three types of MVP estimates

Table 3 Estimates of Minimum Viable Population (MVP) considering only one or various combinations of three types of genetic factors: segregation of recessive (partially) deleterious alleles, loss of adaptive variation and fixation of deleterious mutations by genetic drift.

MVP (Ne)	Genetic effect	Evolutionary forces	Type of genetic variation	Reference
1–50	Segregation	inbreeding	deleterious, recessive alleles (mainly dominance)	(159)
2–500	Loss of variation	mutation, drift	quantitative; all mutations	(91, 159)
2–5000	Loss of variation	mutation, drift	quantitative; quasineutral mutations only; ca. 10% of all mutations	(90)
3–1414–2000[*]	Loss of variation	mutation, drift, stabilizing selection	quantitative; all mutations	(89)
3–4472–10,000[*]	Loss of variation	mutation, drift, stabilizing selection	quantitative; quasineutral mutations only; ca. 10% of all mutations	(89)
4–100–1000's[**]	Accumulation & fixation of mutations	mutation, drift, selection[§]	mildly detrimental mutations with additive effects	(89, 90, 98)
4–100[***]	Accumulation & fixation of mutations & segregation	mutation, drift, selection, inbreeding[§]	mildly detrimental mutations with additive effects plus deleterious mutations with any degrree of dominance	(99)

Arabic number (1–4) preceding MVP indicates criteria to determine MVP as follows: 1-the effective population size (Ne) with a 1% increase per generation in inbreeding coefficeint, 2-Ne in which generation of genetic variation by mutation equals loss of variation by genetic drift, 3-Ne that enables maintenance of 80% or more of the variation with respect to an infinite population, or 4-Ne for which mean time to extinction is in the order of 100 generations. Note that these type-4 etimates are the only ones generated from stochastic population dynamic models that yield probability distributions of times to extinction and actually enable strict population viability analysis. See text for more details.

[*] Low values for house-of-cards model and high value for gaussian model; these are appropriate for loci with strong effects and low mutation rates (few alleles/locus) and for loci with small effects and high mutation rate (many alleles), respectively (see Ref. 90)

[§] Constant growth rate until maximum $N = K$, discrete and non-overlapping generations.

[**] Low values for constant selection coefficients (s) against mildly deleterious mutations (standard deviation/mean = c = 0); high limit for c = 1, that indicate the existence of variance in s.

[***] Constant selection coefficients (c = 0), see[**] for futher explanations.

are based only on population genetic considerations assuming populations at equilibrium. Estimates of effective population size, inbreeding coefficients, genetic variation and structure are useful to evaluate the role of inbreeding depression and loss of potentially adaptive variation in natural populations stressed in 1-3 MVP estimates. We review data on these for TRF trees. All studies have used electrophoretic isozyme loci. DNA-level studies have recently started to appear (66, 162), and these and the analytical tools being developed are promising (113, 151, 153, 154). Studies on genetic variation of quantitative traits are important, but practically absent from the literature of TRF trees (see preliminary results in 84).

Effective Population Size and Genetic Drift

GENERAL THEORY Genetic drift refers to chance fluctuations in allele frequencies due to random sampling among gametes (172). The relative importance of genetic drift compared to other evolutionary forces can be assessed by means of the effective population size (N_e). N_e is defined as the size of an idealized population that would have the same amount of inbreeding (inbreeding effective size) or of random gene frequency drift (variance effective size) as the population under consideration; these two quantities are not necessarily equal, and they differ especially when population size varies (85). The rate of loss of genetic diversity due to genetic drift will be higher in populations with smaller effective sizes, whereas in large populations its effects are negligible. If population numbers are rapidly recovered after a reduction in size, the effects of drift will be smaller than if populations were constantly kept small (14).

In most cases, population size ($N =$ number of reproductive adults) are different from N_e due mainly to fluctuations in population size, high variance in reproductive success, sex ratios different from one, and overlapping generations (38). The N_e/N ratio has been found to vary between 0.25 and 1 for animal species (127). Plants are likely to have low N_e/N ratios because of sessile condition, restricted pollen and seed dispersal, and partial or complete selfing (110). Estimates of N_e assume that a discrete population can be identified. However, it is sometimes difficult to delimit objectively a discrete group of individuals in natural conditions; in this case, information on the size of populations is provided by estimates of neighborhood size (N_b), defined as a group equivalent to a panmictic unit within a continuous distribution of individuals (38). Neighborhood size is related to deme population density by the relationship: $N_b = Ad$, where A is the neighborhood area and d the density of breeding individuals (38).

APPLICATIONS TO TRF TREE SPECIES Unfortunately, few estimates of N_e or N_b exist for plant species in general, and they have been obtained for only five

TRF tree species. N_e estimates vary greatly depending on method as shown in data for only one species (45). Estimates of N_b assume a stepping-stone population structure model and are based on the effective number of immigrants per generation (*Nm*), obtained using Wright's F_{ST} statistic (152). N_b values are: for *A. mexicanum*, 27.84 (many times smaller than direct estimates, 560 and 187) (45); for the canopy tree *Cordia alliodora*, 15–76 (23); for *C. obtusifolia*, 19.4–87.4 (C Lara-Moreno, A Garay, ER Alvarez-Buylla, in preparation); for the lower canopy trees *Psychotria faxlucen*, 70 (45); and for *Combretum fruticosum*, 6 (45). We obtained N_b estimates for another 14 TRF tree species (data from 60): values varied between 15.9 for *Acalypha diversifolia* and 69.8 for *Gustavia superba* and *Quararibea asterolepis*, with a mode around 25.

In an attempt to relate N_e to loss of genetic variation, Hamrick & Murawski (62, also see 117) compared 16 common tropical tree species with 13 uncommon species and showed that less genetic diversity is maintained in less dense populations. They argued that this was due to low effective population sizes of the less common species. However, estimates of N_e were not obtained, and it is not clear what the relationship of the density estimates would be to the species' census and effective sizes. If the population distribution is uniform, then population densities will be partial indicators of neighborhood size.

Breeding and Mating Systems, Inbreeding Depression, and Heterosis

GENERAL THEORY Mating systems determine the mode of transmission of genes from one generation to the next and are thus important factors affecting levels of genotypic variation and its distribution within and among populations. Genetic markers can be used to obtain quantitative estimations of the mating system and of biparental inbreeding of tree species by means of the single (t_s) and multiple (t_m) outcrossing rates (see review in 27, 138). The outcrossing rate can affect the degree of isolation between demes in continuous populations through its effect on the neighborhood area: Low outcrossing rates reduce neighborhood areas, and a maximum neighborhood area is achieved at $t = 1$ (38).

Theoretical and empirical reviews of the relationship between mating systems and inbreeding depression (the reduced fitness of inbred offspring compared with outcrossed offspring) are numerous (32, 83, 93, 141). This is an important issue to consider in conservation genetics because small populations generally undergo inbreeding. High inbreeding levels, however, do not necessarily result in inbreeding depression; levels of inbreeding depression depend mainly on the underlying genetic mechanism and the previous breeding history of the species (14, 32). If the detrimental effects of inbreeding are caused by lethal or deleterious recessive alleles, after prolonged and intense inbreeding most of the genetic load will be purged and inbreeding depression will disappear. Purging, however, is not always feasible (14, see also 90 for other causes that impede purging). If inbreeding depression is caused by overdominant loci, it may increase with the selfing rate. Only in the case of asymmetrical overdominance, inbreeding depression is eventually eliminated due to the loss of less fit alleles (14, 32).

Mechanisms underlying the relationship between heterozygosity and fitness have been the subject of intense research and are still a matter of debate (31, 71, 114). Many animal and plant species exhibit heterosis, in which more heterozygous individuals perform better than more homozygous ones. Two main hypotheses exist to explain this phenomenon: (*a*) overdominance, where heterozygosity per se confers an advantage, and (*b*) dominance, that proposes that more homozygous inbreds are merely expressing a higher proportion of deleterious recessive alleles (57). Smouse (155) proposed a model (the adaptive distance model) to distinguish between these two hypotheses, but similar results can be obtained with either genetic mechanism of heterosis under nonrandom mating (71).

APPLICATIONS TO TRF TREE SPECIES TRFs have high levels of dioecious and self-incompatible, hermaphroditic species, which led to the idea that tropical trees are predominantly outcrossed (15, 16, 17a, 18, 19, 23). Quantitative estimates of the amount of outcrossing further showed that most tropical tree species [studied by means of Ritland & Jain's (138) multilocus mixed-mating method] have high outcrossing rates (t_m) (23, 46, 61, 129, 130; reviews in 58, 61, 97). In some species, however, inbreeding was not negligible (129, 130). Genus-wide (*Acacia*) surveys have revealed variation in outcrossing rates (0.62–0.97) among species (116).

Lowest levels of outcrossing were found for pioneers *Cavanillesia platanifolia*, a canopy tree with hermaphroditic flowers, ($t_m = 0.57$ and 0.35) and *Ceiba pentandra*, ($t_m = 0.689$). These values suggested that early successional, colonizing tropical trees have highly plastic mating systems that ensure seed production when a single individual colonizes a large gap (58). However, the dioecious pioneer *C. obtusifolia* did not show evidence of biparental inbreeding (4) with $t_m = 0.974$ (SE = 0.024). The outcrossing rate in TRF trees was also found to be strongly influenced by nongenetic factors. Trees with lower population densities had lower t_m values than did more abundant species (120), and population reductions in density due to logging were associated with a significantly higher proportion of seeds produced through selfing (118).

Few and scattered data exist on the harmful consequences of inbreeding for TRF trees. In *Acacia mearnsii* and *A. decurrens*, the average height of two experimental groups of selfed progeny was 26% and 15%, respectively, less than open-pollinated controls (115, cited in 57). Inbreeding depression was also evidenced in *A. mangium,* introduced from Australia into Malaysia from a single tree, and in *Hevea brasiliensis* (57).

Heterosis has been documented for only a few tropical species, although it seems to be a widespread phenomenon in forest trees (114). Decreasing fixation indices exist along life-cycles in *A. mexicanum*, *C. obtusifolia*, *Shorea megistophylla,* and *Cavanillesia platanifolia* (3a, 46, 118). In *A. mexicanum*, a positive significant correlation was found between the adults' heterozygosity and trunk growth (46). Smouse's (155) adaptive distance model applied to *C. obtusifolia* suggested that overdominance was the most likely cause of heterosis; however, associative overdominance cannot be completely ruled out as the underlying mechanism (E Alvarez-Buylla, C Lara-Moreno, AA Garay, unpublished information).

Genetic Variation, Population Genetic Structure, and Gene Flow

GENERAL THEORY The most widely used parameters to quantify genetic variation are the proportion of polymorphic loci within species (P_s) and within populations (P_p), and the overall genetic diversity within species (H_s) and within populations (H_p) (59). The distribution of this variation within and between populations can be found by means of Wright's F statistics or Nei's G_{ST}. However, the scale at which the genetic structure of populations is considered is important; patterns may differ depending on the relative importance of factors (mating systems, selection, population size, and pollen and seed dispersal distances) that affect the genetic structure of populations at each spatial scale. Spatial autocorrelation models can be used to assess the fine-scale genetic structure of populations (50, 150). Another method, proposed by Hamrick et al (63), determines the mean number of alleles in common (NAC) for individual pairs at increasing distances.

Theory predicts that in subdivided populations, random genetic drift will result in genetic differentiation among subpopulations (172). Gene flow between these subpopulations, however, will set the limit to how much genetic divergence can occur; reduced gene flow between populations will increase the effects of genetic drift. Several models take into account the effects of gene flow under several assumptions of population structure (152; review in 150). For example, under an island model and at drift-mutation equilibrium, a value of *Nm* greater than 1 will be required to prevent genetic divergence of subpopulations resulting from genetic drift (171). Allendorf (1) further suggests for management purposes that an average exchange rate of exactly one reproductively successful migrant among demes per generation ($Nm = 1$) should be maintained to avoid genetic drift and still enable local adaptation. In two-dimensional stepping-stone models, drift predominates over other forces if *Nm* is much smaller than 1; if it is greater than 4, subpopulations behave as a single panmictic unit (150).

Several indirect methods yield estimates of gene flow (Nm or N_b) (150, 152). In a subdivided population at demographic equilibrium, methods based on Wright's F_{ST} statistic [$Nm = (1 - F_{ST})/(4F_{ST})$] for an infinite population number and an island model provide the most accurate and practical estimates of Nm or N_b (152). Direct methods for estimating gene flow depend on observations of dispersing individuals or gametes; these measure current gene flow rather than average levels of gene flow obtained with indirect methods (see review 150).

APPLICATIONS TO TRF TREE SPECIES The proportion of polymorphic loci within species (P_s) for tropical woody species was found to be high (mean $P_s = 50.6\%$), as well as levels of genetic diversity within species (mean $H_s = 0.160$). Greater proportions of variation were found to be maintained within rather than among populations for tropical species (mean G_{ST}-0.135) (58, 59). The most important determinants of genetic diversity among tropical tree species are the density of populations (62) and geographic distribution (97). The proportions of variation maintained among populations were very low for 10 TRF tree species (average $G_{ST} = 0.05$) (59). *C. obtusifolia* and *A. mexicanum* had also very low levels of among population variation ($F_{ST} = 0.029$ and 0.040 respectively) (4, 46).

Microspatial genetic structure has been documented for a few species. For several TRF trees, Hamrick et al (63) found that near neighbors have more alleles in common than more distant ones; however, family structure disappeared in older life-stages. These patterns were related to the seed dispersal syndromes because NAC values were greater for species with limited seed dispersal. Spatial autocorrelation statistics showed that *C. obtusifolia* has a marked genetic substructure among seedlings within canopy gaps, perhaps caused by limited or correlated seed dispersal; this structure was less evident for older life-stages but was maintained up to the adult stage (B Epperson, ER Alvarez-Buylla, in preparation). Patterns of local genetic structure for this species were further supported by F_{ST} estimates which showed that between-patch (local scale) genetic differentiation was high, suggesting that gap dynamics has significant effects on this species' genetic microspatial structure (3a). The local scale pattern for this species strongly contrasts with macrogeographical patterns (up to 130 km) that did not show significant genetic structuring ($F_{ST} = 0.029$) (4).

TRF trees are pollinated predominantly by animals rather than by wind. However, animal and pollen vectors do involve a wide range of sizes, foraging strategies, and potential for flying long distances. Seed dispersal by animals is also common, although wind or gravity dispersal occur more often (61). Hamrick & Loveless (60) found that the potential for gene movement and

G_{ST} values were highly correlated. These same authors provide Nm estimates based on F_{ST} that ranged from 2.53 for *A. diversifolia* to 11.11 for *Quararibea asterolepis* and *Gustavia superha*. Another method to study gene flow that has been applied to tropical trees is paternity analysis (41). General results show that a great potential exists for long-distance pollen dispersal (review in 126). This and other similar results, obtained by other methods (see above), led Hamrick & Murawski (61) to suggest that effective breeding units for common tropical tree species may be on the order of 25 to 50 ha (126). It is important to note from these results that pollen dispersal may sometimes be restricted. Using paternity analyses Boshier et al (23) found evidence of an increase in localized matings among genetically correlated individuals for *Cordia alliodora*, and S Kaufman, P Smouse, and ER Alvarez-Buylla (in preparation) found that *C. obtusifolia* exhibited a pattern of isolation by distance at a local scale; a greater percentage of matings occurred between near neighbors.

Genetic Effects of Fragmentation and Applications to Conservation

It is a subject of debate in conservation biology whether to keep a single large population or many small populations of total equal size (SLOSS) (149). Which of these strategies is more appropriate for conservation of a particular species will depend on the species biology (breeding structure, mating system, genetic structure, etc).

If populations are subdivided and gene flow restricted, genetic drift may cause genetic differentiation. Small population size (a result of habitat fragmentation) may also increase the number of matings between relatives, thus increasing levels of inbreeding. This may be particularly important in obligate and predominantly outcrossing species, due to the possibility of inbreeding depression. Habitat fragmentation may also cause disruption of pollen and seed vectors, making isolated populations more vulnerable to drift and inbreeding effects. The effects of population subdivision need not result from habitat fragmentation. Isolation will occur if seed or pollen are dispersed over short distances, causing neighborhood areas to be small (e.g. 38). Other researchers have emphasized the beneficial consequences of population subdivision. Under certain circumstances, population subdivision may enhance population survival through the maintenance of genetic variation. Conservation strategies that incorporate this effect for animal species have been suggested (30, 34); however, these must take into consideration the particular biological characteristics of the managed species so as to avoid other possibly detrimental consequences (170a).

To decide what strategy is adequate for a given species, it is relevant to consider genetic data from continuous populations. The effects of fragmentation on population viability will depend on conditions prior to fragmentation (126). Outcrossing rates of tropical trees decrease with decreasing density. Outcrossing species should have high genetic loads, and if a sudden reduction in population size or density occurs, increased inbreeding may lead to inbreeding depression. Negative effects of inbreeding have been reported for some tropical tree species. Tropical tree species should then be particularly vulnerable to changes in density and population size.

DEMOGRAPHIC-GENETIC MODELS

General Theory

Recent theoretical developments that integrate explicit genetic factors to stochastic demographic models are providing new estimates of MVP and important insights concerning the relative role of genetic and demographic factors in determining risk to extinction of populations of different sizes (89, 90, 98, 99, see Table 3). Minimum viable population estimates that stress the accumulation of mutations (4-MVP estimates in Table 3) depend critically on the rate of spontaneous mutation, fitness effects of different mutations, and coefficients of variation of selection coefficients of mildly deleterious mutations (90, 98 and Table 3). All MVP estimates in Table 3 except the first one have used data from *Drosophila melanogaster*. There is much need of this type of estimates for other organisms, particularly for plants (see review in 99). Incorporation of inbreeding depression due to segregation of preexisting mutations does not yield a significant increase in estimates of MVP (see Table 3) (99). Both initial N_e and demographic parameters r and K affect the rate of fixation of deleterious mutations and the population decline to extinction after the population rate of increase has become negative (see also 88 discussed above). Epistatic interactions among mildly detrimental mutations and compensatory mutations at different loci, not incorporated in models, could increase mean times to extinction. However, variance in selection coefficients guarantees that the mean time to extinction is asymptotically proportional to a low power of N_e (90).

These demographic-genetic models (see review in 90) have enabled analyses of how the risk of eventual extinction from fixation of new mutations scales with population size, and how this compares with the risks from stochastic demographic factors. In contrast to previous expectations (87), the fixation of new mildly detrimental mutations may be comparable in importance to environmental stochasticity. Therefore, the effect of this genetic factor implies MVP as large as a few thousands. Both factors imply a power relationship between mean time to extinction and population size. In contrast, demographic stochasticity, inbreeding depression, and fixation of new mutations, assuming constant selection coefficients, determine a nearly exponential relationship between mean time to extinction and population size (see also 98, 99).

Perspectives of Applications to TRF Tree Species

It is clear that the effect of demographic and environmental factors will depend on the details of the life-history of the species being studied, while the effects of genetic factors are more general because of universal genetic laws. Traits of TRF tree species (overlapping generations, response to patch dynamics, population genetic structure at different scales, dioecy, and varying sex ratios) are likely to affect the results of demographic-genetic models. These models should be taken as a basis to analyze the sequential incorporation of these traits. Gene flow among subpopulations as another source of genetic variation is likely to affect the models' outcomes. Analyses will probably have to rely almost entirely on simulations or on transition matrix approaches such as those proposed by Lynch et al (99). This type of stochastic model will enable rigorous PVA for TRF tree species. Experimental plant systems should also be implemented to estimate some of these key parameters. The obvious candidate is *Arabidopsis thaliana*.

The few TRF tree species for which both demographic and genetic data have been obtained help us to illustrate the value of integrating both types of information. For example, the available demographic and genetic results obtained for seed banks of *C. obtusifolia*, show that soil–seed storage in this species has limited demographic relevance, but it is potentially important from an evolutionary standpoint (3, 4, 9). Soon after dispersal, most seeds of this species are eaten by ants; predation rates are density-dependent, however, and the few scattered seeds that remain may survive for long time periods (3, 4). Isozyme data suggest that rare alleles may arise or accumulate among these stored seeds and could constitute a pool of genetic variation not available in any of the other life-stages (9). The other example is that of *A. mexicanum*, for which the availability of demographic and genetic data enabled the first direct estimation of neighborhood size and effective population size in plant species (45).

PERSPECTIVES AND CONCLUSIONS

The deterministic demographic models reviewed here yield generalizations with relevant implications for designing conservation strategies for TRF tree species. Simple Lefkovitch matrix models that have been applied to TRF tree species and their extensions to simulate harvesting regimes show that the species' longevity is a key parameter. In long-lived species later life-cycle stages (preadult and adult) are the most important, while in short-lived species the regenerative phases (seeds, seedlings, and juveniles) are the most critical. For conservation purposes, therefore, the study of the critical life-stages of the species being considered should be emphasized. Metapopulation models suggest that long- and short-lived species will also have contrasting responses to different temporal and spatial regimes of perturbation. However, future developments of metapopulation models for TRF tree species should consider dynamics that result from regional fragmentation regimes caused by deforestation by humans and stochastic fluctuations of the patch-dynamics regime (24, 88). The possibility of aging and of locating past treefalls at Los Tuxtlas make this forest an ideal model study site to address questions on the effects of long-term gap dynamics on persistence of species with contrasting life histories (106). Finally, density-dependent factors seem to be important in regulating populations of at least the most abundant species. However, sporadic catastrophic events seem to maintain populations fluctuating in a density-independent fashion with densities below their carrying capacities.

Such catastrophic events are of a stochastic nature, and their impact on population long-term viability should be considered in more detail in future models. Only one demographic study has performed population viability analysis for four TRF tree species using the simplest linear Lefkovitch matrix model. Its results agree with those derived analytically for nonstructured populations. Hence, more elaborate stochastic analytical theory might guide further analyses of the effect of demographic and environmental stochasticity on determining extinction times of TRF tree species. We have emphasized that quantitative evaluations of the relative effects of the key factors affecting TRF tree populations should be based on comparisons of model outputs with contrasting assumptions, rather than on comparison of field data with outputs of single models. The obvious next step is to extend this approach by incorporating the effect of different types of stochasticity to perform more realistic viability analyses of TRF tree species.

The use of classical population genetic models has shown that (*a*) TRF tree species possess high levels of genetic variation; (*b*) most of their variation is found within rather than among populations; (*c*) such species are predominantly outcrossed; and (*d*) they have high levels of gene flow. These results and neighborhood size-estimates suggest that TRF tree species have large effective population sizes. Hence, genetic drift is not expected to play an important role in the evolutionary dynamics of the type of TRF tree species studied up to now (59). Therefore, under present conditions, genetic factors do not seem to be critical for the long-term persistence of TRF tree species. However, drastic population reductions due to fragmentation are likely to have strong impact because of the high genetic load kept by most TRF tree species. Also, the correlations between the genetic structure and the type of dispersers and pollinators support the idea that conservation plans of TRF trees should keep in mind the effects of fragmentation regimes on animal vectors (96, 126). Regional analyses of population structure also suggest that preserving a few populations would ensure the conservation of most genetic variation existing in these species (58). However, recent studies are revealing significant genetic structuring at microspatial scales that may result from the action of important ecological factors such as seed dispersal modes and gap dynamics. The latter results imply that several of such local populations should be preserved.

The specifications of the models and the values of the parameters used determine the MVP estimates reached, which vary from 50 to more than 1000 individuals. Therefore, details of the natural history of species and accurate estimates of parameters may be crucial for establishing realistic demographic-genetic models that provide useful MVPs for guiding conservation decisions (24, 149). However, time and resource limitations hinder long-term exhaustive studies of many species. Therefore, we suggest that detailed, rigorous, and standardized studies of model systems should be pursued. These will provide guidelines of key demographic-genetic factors and conservation priorities for different types of TRF tree species. TRF tree species may be arranged along a continuum of life history (i.e. demographic and genetic traits) types (8, 105). Species of similar types along such a continuum should share traits that may determine their population and evolutionary dynamics and their response to disturbance. We have chosen to study the extremes of the continuum: the pioneer *C. obtusifolia* and the long-lived palm *A. mexicanum*. The results reviewed here for these two species clearly show their contrasting demographic and genetic dynamics.

Present models do not enable evaluations of the relative importance of demographic and genetic factors in the long-term persistence of TRF species with contrasting life histories. Rigorous demographic-genetic models (89, 90, 99, 100) that incorporate population substructuring and gene flow should aid in resolving the effect of fragmentation on the long-term subsistence of TRF tree populations. A general conclusion from demographic-genetic models and empirical evidence that should apply to TRF tree species is that, in large populations that are suddenly reduced in size, inbreeding depression based on segregating detrimental mutations carried by the founders constitutes an important risk of rapid extinction (90, 159). More gradual population reduction will make fixation of new detrimental mutations a more serious risk of eventual extinction (90).

Most remaining natural TRF areas are very reduced in size and many of them are highly fragmented (168). This situation is likely to worsen due to the pressure that human populations are exerting on natural resources because of the unequal distribution of wealth and technologies among and within countries and social groups, because of market and institutional failures and the consequent inefficiencies in resource management (20, 54, 138a, 161). In this scenario it is not conceivable to think of long-term conservation of untouched, large, and continuous forested areas. Present conservation plans should be concerned with the demographic and genetic consequences of forest fragmentation and the design of plans of sustainable management for ecologically or economically key species.

Most TRF tree species are rare and large areas seem to be required to meet even the most modest MVP estimates (see Tables 1 and 3). Most demographic and genetic studies, however, have been performed for abundant species. It is urgent to have model systems of the group to which most TRF tree species belong: long-lived and rare, and/or long-lived and fragmented. From the demographic perspective, for example, it is important to establish density-dependent factors that may be important at a local scale and that may regulate these species' populations, of which many have clumped distributions. From the genetic perspective, for example, it would be important to document effective population sizes of this type of species with different degrees and patterns of fragmentation. Finally, however powerful the population approach may be, conservation and management strategies of natural complex systems should keep in mind the question of how independent the dynamics of single species populations are. The "equilibrium" and "non-equilibrium" hypotheses of community structure and dynamics constitute contrasting ecological scenarios (37, 79, 80) and suggest two different strategies and challenges concerning the conservation of TRF. In the equilibrium scenario, conservation programs directed to preserve particular species without consideration of other species may not be appropriate because we expect a stable system in equilibrium, in which complex biotic interactions have evolved for long periods of time and yielded an equilibrium in a coevolved complex of species. However, these same conditions could determine lower MVP, and species with fewer individuals could be preserved for long periods. In the non-equilibrium scenario, we may assume more independent dynamics and population models may be particularly appropriate. For such systems, the challenge would be to conserve dynamic systems that maintain, at any particular time, a high tree diversity; but the specific composition would change randomly as a result of stochastic loss of species and origin of new ones.

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