

A STOCHASTIC MODEL FOR THE EXTINCTION OF TROPICAL ORCHIDS

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ABSTRACT. It is possible to produce a model that predicts both the total loss of species as well as the current rates of species extinction based on the distribution of narrow endemic species and estimated rates of deforestation. Twenty-one taxa covering 17 orchid genera were selected and their distributions in terms of recorded localities were determined. These taxa covered 1,421 species of which 539 (37.9%) were narrow endemics found in only one restricted locality. An additional 268 (18.8%) and 163 (11.5%) species were reported from only two and three localities, respectively. Values for species occurring at more than three localities were not considered. The estimated global forest conversion rate used was 0.7% per year, with 45% of tropical forested lands having been cleared at the present time. Using 25,000 as the total global number of orchid species one can estimate that 5,477 (21.9%) of the orchid species have been lost at the present time, and of the remaining species, approximately 55 will be lost each year if current forest conversion rates continue. Madagascar may be an ideal case to test this model. The island's orchid flora is relatively well known and thought to contain about 1,000 species. Analysis of eight taxa showed that 62% were reported from only one locality, 17% from two localities and 7% from three. Using the recent estimate of the 66% total loss (Green & Sussman, 1990) for eastern rainforests for the entire island, the model predicts that 503 species are already extinct. Using the more common estimate of 90% forest loss, nearly three-quarters (747 species) of the island's orchid species should now be extinct.

Un modelo de predicción para la extinción de epífitas tropicales.

RESUMEN. Es posible construir un modelo que predice tanto la pérdida total de especies como las tasas de extinción actuales basado en la distribución de especies endémicas y las tasas estimadas de deforestación. Para ello, se utilizaron 21 taxas de orquídeas que abarcan 17 géneros para los cuales, se determinaron sus distribuciones en base a las localidades registradas. Estas taxas están compuestas de 1,421 especies de las cuales 539 (37.9%), fueron endémicas siendo restringidas a una sola localidad. Otras 268 (18%) y 163 (11.5%) fueron ubicadas en dos o tres localidades respectivamente. Las especies encontradas en más de tres localidades no fueron consideradas. La tasa estimada de conversión forestal global utilizada fue 0.7% por año, reflejando el 45% de los bosques tropicales deforestados en la actualidad. Usando 25,000 como el número total de especies de orquídeas, uno puede estimar que 5,777 (22.9%) de las especies de orquídeas se han perdido hasta el presente, y de las especies restantes, aproximadamente 55 se perderán cada año, si la actual tasa de conversión de bosque continúa. Madagascar, puede ser un caso ideal para probar este modelo. La flora de orquídeas de la isla es relativamente bien conocida y se considera que está compuesta por unas 1,000 especies. El análisis de 8 taxa demostró que 62% tenían registros para una sola localidad, el 17% para dos y 8% para tres. Usando la más reciente estimación para la pérdida total para los bosques tropicales de oriente, 66%, el modelo predice que unas 503 especies y están extintas en la isla. Usando un estimado más utilizado señala un 90% de pérdida del bosque, y por ello casi tres cuartas partes del total de especies de orquídeas (747) de la isla deben estar ya extintas.

INTRODUCTION

The effects of deforestation and subsequent rates of plant extinction have recently been called into question (Lugo, 1988) and there is a need for more accurate assessments of the problem. Three types of models have been used to predict extinction rates in organisms. The first of these is the "Island Law" of biogeography, originally promulgated by MacArthur and Wilson (1967) and later used effectively by others. Simberloff (1986) used that model to propose that 15% of all plant species would be lost by the turn of the century. A second set of models are demographic and based on birth and death rates (Belovsky, 1987; Ewens *et al.*, 1987; Goodman, 1987). Third, there are stochastic models which consider cat-

astrophic chance events that could wipe out an entire population. Few if any, of these models have been used to make predictions about extinction rates of specific groups of plants.

The model presented in this paper is based on a simple stochastic premise suggested by Wilson (1988). He asserted that the number of species lost is in direct proportion to the amount of tropical forest converted. He estimated that if there were 5 million species in the tropics, that approximately 17,500 species would be lost yearly. This figure is based on the assumption that half of the tropical species ($0.5 \times 5 \times 10^6$) are extremely localized. It is this fraction that is vulnerable and could be lost. Multiplying the annual tropical forest conversion rate by the number of

narrow endemics would give the number of species obliterated each year, purely by chance. Wilson used a conservative 0.7% as the fraction of remaining forest currently being cut each year.

There are several problems in using this model, one of the most difficult being the distribution profiles of tropical species. It is not clear that half of the tropical species are, in fact, narrow endemics. There appear to be few studies published on the amount of endemism in tropical plant families. Knowledge of the numbers of species that occur in single or several disjunct populations are needed to run a stochastic model. Another problem concerns the actual rates and patterns of land conversion; it is extremely difficult to get precise and up-to-date information on real deforestation rates.

Orchidaceae is the largest family of flowering plants and for conservation purposes they make an ideal "flagship" group with which the public can readily identify. In addition, these plants form an important but little-acknowledged part of the biodiversity of tropical forests. In the La Selva forest in Costa Rica, the Orchidaceae form the largest family of flowering plants, in terms of numbers of species (Hammel, 1990). On Barro Colorado Island, Panama, the orchids are the second largest component of the flowering plant families (Foster & Hubbell, 1990). The Orchidaceae rank fourth among the flowering plant families in the Manu floodplain forests of southeastern Peru, but they are the largest component in terms of epiphytes in that forest (Foster, 1990). Even in central Amazonia, where the family is only listed thirteenth in abundance, it is the largest component of biodiversity among the epiphytes (Prance, 1990).

Orchid plants have an aura of exoticism with which lay people readily identify. Furthermore, because of the intense interest by amateur collectors and gardeners, an enormous library of knowledge has been built up concerning orchid taxonomy and species distributions. On a worldwide basis, this is probably much greater than that available for any other large tropical plant family. Within this literature are some of the data that can be used to determine current extinction rates among the Orchidaceae using a refinement of Wilson's model.

The Model

In the present model, the probability of a species suddenly becoming extinct is considered as the stochastic chance of the area occupied by the species being obliterated due to land conversion. The model formally is:

$$E = (ab_1c) + (ab_2c^2) + (ab_3c^3) + \dots$$

where E is the number of extinct species; a is number of species in the taxon; b_1, b_2, b_3, \dots the proportion of species in the taxon that are distributed in 1, 2, 3, . . . localities, and c is the land conversion factor. The land conversion factor can either be the total proportion of land converted or a conversion rate per unit time.

Assumptions

In order to use this model to calculate extinction rates of orchid species, it is necessary to make several assumptions.

A. NUMBER OF SPECIES. The first assumption concerns the total number of species in the Orchidaceae. The numbers are confounded by two factors, the amount of synonymy in the groups and also the numbers of species that have yet to be recorded and named. Numbers available in the literature range quite widely with the highest being approximately 35,000 (quoted in Atwood, 1986). Hendrych (1985) used the Index Kewensis to estimate 17,651 known species. Similarly, Atwood (1986) determined 19,128 species of orchids and estimated that no more than 23,000 species existed, considering claims of 25,000 species as being improbable. Dressler (1981) suggested that there might be 19,192 orchid species. It is often stated that approximately 10% of the flowering plants are orchid species (McMahan & Walter, 1988) and a common estimate of 250,000 flowering plant species is given as the size of that taxon. Hendrych (1985) calculated from the Index Kewensis that 286,765 species resided in the Magnoliophyta. This would place the orchids as only 6.2% of the flowering plants.

For those orchid genera which have received intense amateur attention during the last twenty five years, a surprisingly large numbers of new species have been discovered. The genus *Paphiopedilum* has received much attention. Cribb (1987) rather conservatively recognized 60 species in that taxon, and of those, 15 had been described since 1965. In the last four years an additional three "good" species have been described. Thus, since 1965, an additional 23%, in terms of numbers of species, have been described. In the central African *Bulbophyllum*, an additional 22.2% of the species were described after 1965 (Vermeulen, 1987). The Brazilian rupicolous *Laelia* (Withner, 1990) yielded 21 new species (35.5% of the total genus) after attention was focused on that group. In addition, very large numbers of new species in the Pleurothallidinae have also been described in recent years (Luer, 1986, 1988a, 1990). If these patterns hold for the orchids as a whole, then 25,000 species for the

TABLE 1. Global distribution of orchid species. B₁, B₂ and B₃ refer to narrow endemics, bi- and tridisjunct species, respectively. Note that Madagascan orchids are not included.

Genus	No. species	B ₁ (%)	B ₂ (%)	B ₃ (%)	Location	Source
<i>Bulbophyllum</i>	29	4 (14)	0 (0)	3 (10)	E. Africa	3
<i>Bulbophyllum</i>	66	17 (25)	5 (8)	5 (8)	Africa	14
<i>Bulbophyllum</i>	96	29 (30)	21 (20)	17 (18)	Thailand	12
<i>Bulbophyllum</i>	159	109 (69)	25 (16)	13 (8)	Madagascar	9
<i>Cymbidium</i>	18	2 (11)	4 (22)	0 (0)	Thailand	12
<i>Dendrobium</i>	31	1 (3)	2 (6)	1 (3)	New Guinea	10
<i>Dracula</i>	30	12 (40)	6 (20)	6 (20)	Trop. Am.	8
<i>Elleanthus</i>	34	11 (32)	9 (26)	4 (12)	Peru	11
<i>Epidendrum</i>	170	67 (39)	28 (16)	24 (14)	Peru	11
<i>Jumellia</i>	44	27 (61)	10 (22)	5 (11)	Madagascar	9
<i>Masdevallia</i>	210	98 (47)	47 (22)	21 (10)	Trop. Am.	6
<i>Masdevallia</i>	36	15 (42)	9 (25)	5 (8)	Peru	11
<i>Maxillaria</i>	97	48 (49)	18 (19)	8 (8)	Peru	11
<i>Microcoelia</i>	26	3 (12)	2 (8)	1 (0)	E. Africa	5
<i>Oberonia</i>	41	5 (12)	10 (24)	5 (12)	India	1
<i>Odontoglossum</i>	58	8 (14)	14 (24)	12 (19)	So. Am.	2
<i>Phalaenopsis</i>	44	10 (23)	12 (28)	7 (16)	S.E. Asia	13
<i>Pholidota</i>	29	5 (17)	3 (10)	2 (7)	Asia	4
<i>Polystachya</i>	89	22 (25)	15 (17)	14 (16)	E. Africa	3
<i>Scaphosepalum</i>	30	11 (37)	6 (20)	3 (10)	So. Am.	7
<i>Stelis</i>	84	35 (42)	22 (25)	7 (8)	Peru	11
Totals	1,421	539 (38)	268 (19)	163 (12)		

1 = Ansari and Balakrishnan (1990); 2 = Bockemuhl (1989); 3 = Cribb (1984); 4 = De Vogel (1988); 5 = Jonsson (1981); 6 = Luer (1983–1987); 7 = Luer (1988b); 8 = Luer and Escobar (1989); 9 = Perrier (1941); 10 = Reeve and Woods (1989); 11 = Schweinfurth (1958–1961); 12 = Seidenfaden and Smitinand (1961); 13 = Sweet (1964); 14 = Vermeulen (1987).

entire taxon may not be unreasonable and could even be conservative. I have therefore used that number in my calculations.

Both Atwood (1986) and Kress (1986) calculated that 73% of the orchid species are epiphytic. The distributions of terrestrial orchids as compared with epiphytic species are only poorly understood at this time, but it is possible that different patterns of distribution occur depending on growth habit.

B. DISTRIBUTION. To obtain distribution data, I used published herbarium localities from a variety of monographic references (TABLE 1). Some data also came from locality maps published with those monographs. Distributions have been divided into “narrow endemics” (species recorded from only one locality), “bidisjunct species” (species recorded from two discrete localities) and “tridisjunct species” (species from three discrete localities). Species recorded from more than nine localities were lumped together (FIGURES 1, 2). For calculations only the first three categories were used. Species occurring in more than three sites contribute little towards the extinction numbers.

Interpretation of recorded localities is sometimes difficult. Some locality data are very precise and detailed but in other cases, the locality

may have been recorded in much broader terms, sometimes even simply by a country name. Place names also change or are written differently in unfamiliar languages. Different sides of the same mountain or valley have been given different names. Unless one is intimately familiar with the geography of the region, errors can ensue. For this reason, wherever the localities are unclear, I have deliberately erred on the conservative side, i.e., two closely similar names are taken as two separate localities rather than one. This tends to deflate the extinction rates.

Another part of this assumption concerns the area occupied by the discrete population. One would expect that some species might only occur in small patches, while others could be broadly scattered over wide-ranging areas. In all cases of narrow endemics, bi-, and tridisjuncts, I assume that the area occupied by a population is less than the area deforested during the extinction episode under consideration.

C. RATES OF DEFORESTATION. Rates of forest conversion are highly variable from region to region, and obtaining current and reliable information is extremely difficult. In this model, I define deforestation as land use which involves clear-cutting and assume that significant remnants of forest do not remain. Lugo (1988) has

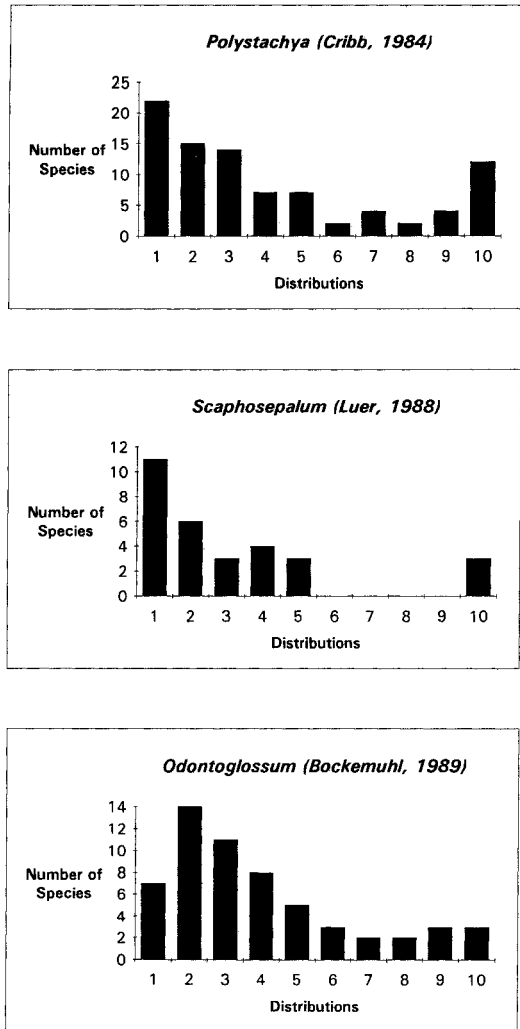


FIGURE 1. Representative distributions of three continental orchid species. Y axis represents the number of individual species for each distribution category. Distribution refers to the number of localities in which the occurrence of a particular species was cited.

pointed out that even with a 99% reduction in Puerto Rican rainforests, the trees that remain in coffee plantations and secondary forests can act as refugia for various species. In those situations, the populations could be reduced to the point where inbreeding depression is inevitable or the pollinator lost. Thus, despite the fact that occasional specimens of a species can be found and they could persist for extended periods of time, depending on the species' longevity and mode of reproduction, those species are functionally extinct.

As this model is oriented towards a global per-

spective, a deforestation rate of 0.7% has been assumed following Wilson (1988). This rate is quite conservative compared to other rates that have been suggested (Myers, 1984). If the actual area converted each year is a constant, then the percent cleared per annum would actually increase, assuming that new forests are not replacing those cut. If one assumes that primary forests now cover only 9 million square kilometers or less (Myers, 1984) and that the original area was 16 million square kilometers (Mabberly, 1983; Gradwohl & Greenberg, 1988), then approximately 43% of the original tropical forested areas have already been cut. As most of the available data are out-of-date, an estimate of 45% of the forested area has now been cleared or degraded is assumed.

RESULTS

Species Distributions

Representative distributions obtained from several different genera are in FIGURE 1. Data for 17 genera representing approximately 5% of the orchid family are summarized in TABLE 1. From these data, it appears that there is only a single case, *Dendrobium* sect. *Oxyglossum* (Reeve & Woods, 1989), with less than 10% of its species being narrow endemics (FIGURE 2). The percentage of narrow endemic species within a genus ranges from 3% to 69%, with the highest being the Madagascan species of *Bulbophyllum* (FIGURE 2). These appear to have much more restricted distributions than *Bulbophyllum* species that occur on the African mainland or in Asia. Of the genera presented in TABLE 1, 539 species (37.9% of the total number of species) are narrow endemics. Bidisjunct species occur in 18.8% of the cases and tridisjuncts (163 species) account for a further 11.5%. In all, some 970 species from this group are found at three or less sites. Thus 68% of the orchids in this survey could be considered to have restricted distributions.

If these numbers are substituted in the extinction equation as the appropriate b values, with 25,000 as the original number of orchid species and a rate of 45% of the tropical forests already converted, approximately 5,477 species should have become extinct by this point in time, i.e., 21.9% of the total family on a global scale.

It is also possible to use the equation to derive periodic extinction rates within the family. Following each extinction period, the rates and numbers will change and calculations become somewhat more complex. In essence, the extinction rate will be the number of species remaining in the taxon multiplied by the proportion of species in each distribution category multiplied by

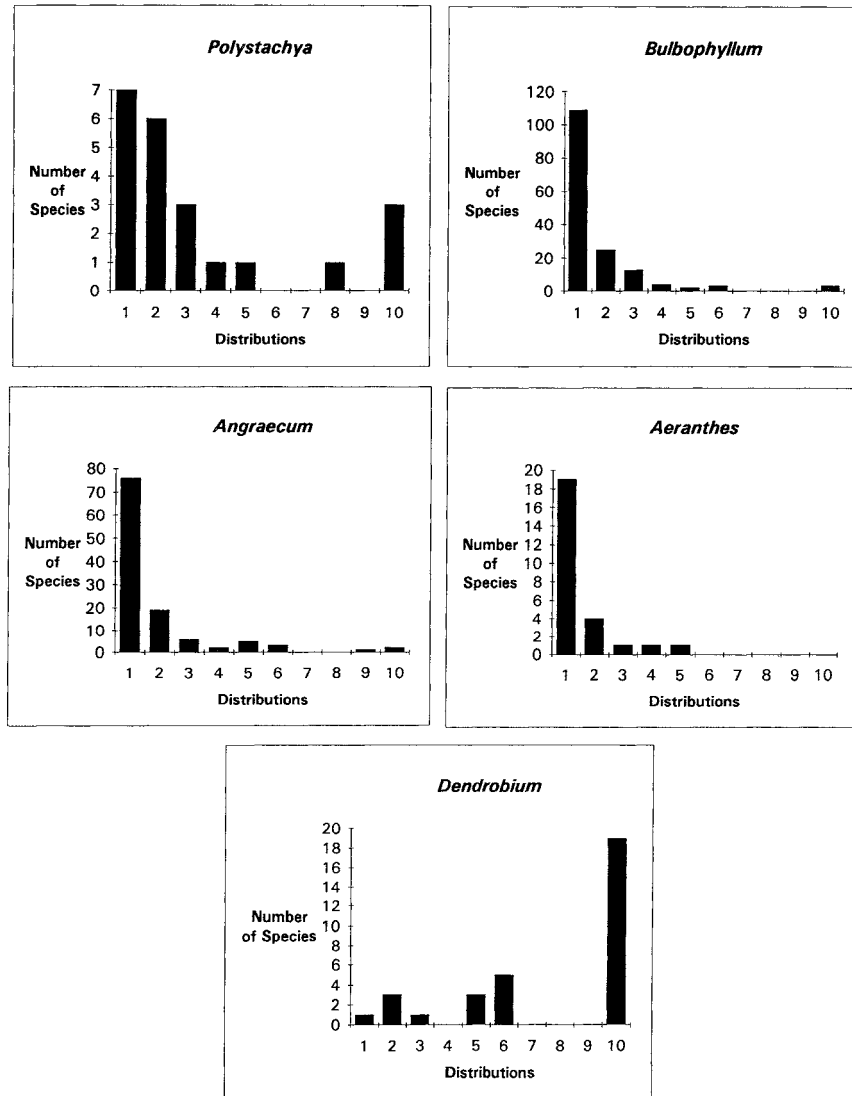


FIGURE 2. Distributions of some island species. *Polystachya*, *Bulbophyllum*, *Angraecum*, and *Aeranthes* represent genera from Madagascar, data from Perrier (1941). *Dendrobium* data from Reeve and Woods (1989) for New Guinea. Y axis is number of species in each distribution category. Distribution refers to the number of localities in which the occurrence of a particular species was cited.

the conversion rate per unit time. Following each period, the number in each distribution category will change not only because some will have been lost, but also because additional species will have been added to it from other distribution categories.

The number of narrow endemics after the first extinction episode will be

$$N_1 = a(b_1 - b_1c + b_2c + b_3c^2 + \dots)$$

and the new b_1 value for narrow endemics will be

$$b_1 = N_1(a - E)^{-1}$$

where N is the number of species in a distributional category and E is the previous decrease in total number of species due to extinction. Likewise, the new numbers of bidisjunct species will be

$$N_2 = a(b_2 - b_2c^2 + b_3c + \dots)$$

and the new b_2 value is similarly

$$b_2 = N_2(a - E)^{-1}.$$

TABLE 2. Distribution of Madagascan orchids. B₁, B₂ and B₃ refer to narrow endemic, bi- and tridisjunct species, respectively. Data derived from Perrier (1941).

Genus	No. species	B ₁ (%)	B ₂ (%)	B ₃ (%)
<i>Aerangis</i>	23	12 (52)	4 (17)	2 (9)
<i>Aeranthes</i>	26	19 (73)	4 (15)	1 (4)
<i>Angraecum</i>	114	76 (67)	19 (17)	6 (5)
<i>Bulbophyllum</i>	159	109 (69)	25 (16)	13 (8)
<i>Cynosorchis</i>	80	41 (51)	13 (16)	4 (5)
<i>Disperis</i>	17	9 (53)	3 (18)	1 (6)
<i>Jumellia</i>	44	27 (61)	10 (22)	5 (11)
<i>Polystachya</i>	20	7 (35)	6 (30)	2 (10)
Totals	483	300 (62)	84 (17)	34 (7)

On an annual basis, the contribution of the tridisjunct species become quite small and can be dropped from the calculations.

Following the loss of 45% of the world's forests, the new numbers and proportions of orchid narrow endemics and bidisjuncts should be: 7,908 (40.5%) and 6,663 (34%) respectively. Using those values and a remaining total of 19,524 species with an annual forest conversion rate of 0.7% approximately 55.3 orchid species should be lost in the first year following the 45% forest conversion. The numbers of extinct species contributed by both the bidisjuncts and the tridisjuncts are less than one and can be disregarded.

Species Losses on Madagascar

The approach outlined here to make global extinction estimates can also be used to calculate the species losses for smaller geographic areas. The island of Madagascar provides an example with the requisite data. The orchid flora of Madagascar was monographed by Perrier (1941). In general, levels of restricted endemism appear to be so much higher in Madagascar than elsewhere that I excluded most of the genera from TABLE 1, as they would bias the data on the liberal side. Instead, the Madagascan genera are presented separately in TABLE 2 and a few representative genera displayed in FIGURE 2. Eighty-seven percent of the Madagascan species are restricted to three or fewer sites, a factor that makes this component of the Madagascan flora particularly vulnerable, in the light of the devastating deforestation rates on that island (Green & Sussman, 1990).

It has been suggested that approximately 1,000 species of orchids exist on Madagascar. The entire island was once covered with forests, but less

than 10% of the forest cover remains today. Of the eastern rainforests, some 34% remain uncut (Green & Sussman, 1990). Using a conservative forest conversion total of 66% for the entire island, 503 (about half) of the species should now have disappeared. A 90% conversion total would indicate a devastating loss of 747 species at this point in time.

DISCUSSION

This model predicts that on a global basis, slightly more than one in five wild orchid species have probably already disappeared from the wild or else are at the point where extinction is inevitable. If the distributions of other plant families follow those of the orchids, then predictions that we might lose 20% of the world's flowering plant species by the turn of the century are conservative. We have reached that point ten years earlier than predicted. Annual rates of orchid extinction are predicted to be about one species per week. If similar rates apply to the rest of the plant kingdom then one to two plant species are being lost each day. The model presented here does not indicate sharply escalating plant extinction rates and such rapid escalations would not be expected until the last fragments of forest are degraded.

Unlike many other extinction models, this model can be tested in the field. If locality data that predate major deforestation epics for a country are available then sampling of randomly selected localities should yield information about the accuracy of the model. For example, examination of the sites of a randomly selected number of Madagascan narrow endemic species, as recorded by Perrier (1941), should reveal that approximately 90% of the sites no longer exist and their orchid flora should also have banished. Similarly, data from Schweinfurth (1958-1961) on Peruvian orchid species could also be used, provided one has good data on Peruvian deforestation.

Field data collected to test the model may be biased. It may happen that orchid species with restricted distributions are not placed independently of each other or the environment. Their placement could conform to certain ill-defined and poorly understood biogeographical parameters. Additionally, deforestation itself may be dependent on several non-random factors such as distance from population centers and steepness of terrain or even tree species composition within the forest. While deforestation localities and orchid species habitat preferences may well be independent variables, too little data exist to verify those relationships. Presumably, the wider

the sample, the less the tendency for error. On a global scale, these biases are probably less important than they would be if potential extinction rates within a single country or geographic area were examined.

The model makes other predictions about the future of the Orchidaceae. Species that are generalists and widespread will survive over narrow endemics that are specialized in discrete habitats. One can therefore expect that a form of artificial selection for generalist orchid species has already occurred. We may end up losing one of the special attributes of the orchid family, its exuberance in producing myriads of unique floral specializations and adaptations.

Generalist species, which are widespread, will not be affected by deforestation until substantial portions of the lands have been converted. More than 95–99% of the land would need to be converted before the generalists are affected. Those species will probably not die out because of stochastic events, but rather because of demographic or area problems that lead to inbreeding depression or inability to achieve pollination. Where the cut occurs between events predicted by the model presented here and those of other models still needs to be investigated.

Predictions from this model depend heavily on the levels of endemism recorded for various species, which rests on the concept of species and their limits. "Splitters" will produce large numbers of species and hence higher proportions of taxa with restricted distributions. The levels of endemism recorded from Madagascar (FIGURE 2, TABLE 2), which seem much higher than those reported elsewhere, could be due to designating variants as species. Despite the current attention focused on Madagascan flora, we may never know the true situation because discrete variants should suffer similar extinction spasms to which the species would be subjected. Conversely, section *Oxyglossum* of *Dendrobium* from the South Pacific had the lowest number of restricted endemics (FIGURE 2). Examination of the history of the *Oxyglossum* taxon (Reeve & Woods, 1989) reveals that of a total of 113 species names, only 28 were retained as "good" species. The reduction in species numbers in Reeve and Woods' revision is much greater than that of other recent revisions in additional *Dendrobium* sections (Cribb, 1983, 1986). They used a much broader species concept than other taxonomists, and recognized taxa at the subspecies level rather than the species level. This could have resulted in the subsequent skewness in distribution. Presumably the true situation for the family lies somewhere between the extremes of these two distribution patterns.

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