to meet the IUCN-proposed 10% expansion target of protected areas, would be the massive sequestration of newly accessible public lands into strictly protected areas, extractive reserves and sustainable forestry areas (National Forests). This would reduce the supply of free-for-all forest resources in public lands, which are likely to continue to attract 'cut and run' logging operations. A recent study has shown that nature reserves greatly reduce local deforestation rates, even if they exist only 'on paper' and are yet to be implemented in practice[15]. Zoning regulations in the Amazon urgently need to be reorganized from a historically messy land titling system and need to include many more large forest reserves under varying degrees of protection ranging from people-free parks to areas under benign forms of exploitation. The private timber industry also needs to be severely restricted through steeper taxes and enforceable penalties, which could help fund field operations deployed by financially frail environmental agencies.

Although Brazilian legislators can pride themselves in having a highly sophisticated set of environmental laws, such laws tend to lack teeth in the vast Amazonian frontier. Haphazard frontier expansion without commensurate investments in government institutions to effectively enforce conservation legislation only perpetuates the boom and bust cycle that will continue to impoverish both the biota and rural population of the Amazon.

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The use and abuse of population viability analysis

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A recent study by Brook *et al.* empirically tested the performance of population viability analysis (PVA) using data from 21 populations across a wide range of species. The study concluded that PVAs are good at predicting the future dynamics of populations. We suggest that this conclusion is a result of a bias in the studies that Brook *et al.* included in their analyses. We present arguments that PVAs can only be accurate at predicting extinction probabilities if data are extensive and reliable, and if the distribution of vital rates between individuals and years can be assumed stationary in the future, or if any changes can be accurately predicted. In particular, we note that although catastrophes are likely to have precipitated many extinctions, estimates of the probability of catastrophes are unreliable.

Population viability analysis (PVA) is a modelling tool that estimates the future size and risk of extinction for populations of organisms[1,2]. PVA works by using life-history or population growth-rate data to parameterize a population model that is then used to project dynamics and estimate future population size and structure[3]. User-friendly PVA software packages allow conservation managers to predict future population sizes and risks of extinction for any population they choose[3]. Because of this ease of application of PVAs, it is important to determine and understand the limits to their predictive accuracy[1,4–6]. Brook *et al.* have tested the predictive accuracy of PVA using data from many populations and conclude that PVA is not a useless tool, and that it should not be dispensed with in favour of alternative untested methods.

Do PVAs work?

The predictive accuracy of a PVA will depend on the purpose to which it is being applied. In practice, there has been a range of alternative uses. PVAs can be used to: (1) predict the future size of a population[1,5,6]; (2) estimate the probability of a population going extinct over a given time[5]; (3) assess which of a suite of management or conservation strategies is likely to maximize the probability of a population persisting[7]; and (4) explore the consequences of different assumptions on population dynamics for small populations[8]. In reality, only the predictive accuracy of the first two cases is estimable, as there are rarely sufficient replicate populations from which to collect data to determine whether the comparative predictions of the third use are accurate, and the fourth use has not generated testable predictions.

There are two ways that the predictive accuracy of PVAs can be assessed. The first approach is to use historical data and, at a point in the future, predict the population size and compare this to what actually happened. To avoid circularity, the data used to parameterize the model should not include data from the time-period over which predictions are made. The

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observed population size (or sizes where the whole population exists as a suite of spatially structured local populations) can then be compared to the distribution of predicted population sizes from the model projections. As well as comparing population sizes, the distribution of observed and predicted population growth rates can also be examined. There are however potential problems with these methods [9].

A second approach is to compare the observed distribution of population sizes with the estimated distribution of quasi-extinction rates. Extinctions are rare, and any individual population can go extinct only once, so it is not possible to compare a probability of extinction with whether a population went extinct. However, quasi-extinction events can be assessed, both in theory and in practice [10], when the population falls below a specified threshold. Many different thresholds can be defined for the same population. In a sufficiently long time series, the observed distribution of population sizes can be compared with the observed distribution of quasi-extinctions from PVA models generating multiple simulated time-series of the same length[1].

There have been few empirical attempts to verify the accuracy of PVAs; the analysis using the most populations (and species) was that of Brook *et al.*[1]. Here, 21 populations from many taxa (eight bird species, nine mammal species represented by 11 populations, one reptile species and one fish species) for which ten or more years of data existed, were selected. Data from the first half of each study were used to construct age-structured population models that were used to generate predicted dynamics for the second half of each study. Brook *et al.* used a comparison of observed and predicted quasi-extinction risks for each population, the simulated mean and observed population growth rate and the observed and mean predicted population size for the last point in each time-series to test the performance of PVAs. The final sentence of their abstract concludes, 'PVA is a valid and sufficiently accurate tool for categorizing and managing endangered species'. The case studies they chose for their analyses were long term and not typically from populations of endangered species, data were of high quality and only one population went extinct; given this biased sample, therefore, this statement is too strongly worded. A statement towards the end of the paper does provide the caveat that 'PVA predictions are surprisingly accurate, given adequate data'; however, there is a risk that a myth stating that PVA nearly always works will become established. So what are the necessary conditions for the predictions of PVAs to be accurate?

Circumstances when PVAs could predict future dynamics

Brook *et al.'s* conclusions[1] could only be valid if two criteria are met – the authors briefly mention both in their paper but do not discuss them in detail. First, data have to be of sufficiently high quality that the estimates of the shape, mean, temporal variance and autocorrelation (that could be caused by density-dependent processes) of the distribution of vital rates, or the population growth rate, are accurate. Second, the future mean and variation of vital rates or the population growth rate will have to be similar to those observed during the period when the data were collected.

Criterion one: data quality

The first of these criteria will only be met in a handful of cases where a large amount of information is known about the biology of the target species and population. The amount of data required will vary among species and among populations experiencing different biotic and abiotic factors. Consider how much data would be required to model a long-lived species in which high recruitment events may only occur once every two to three decades or more (e.g. radiated tortoises, *Geochelone radiata*). A distribution of recruitment rates parameterized from a ten-year period when a high recruitment event did not occur would lead to an overestimate of the probability of quasi-extinction and the population growth rate. However, a distribution parameterized from an equivalent period when a high recruitment event did occur, would lead to an underestimate.

For populations embedded in a spatially heterogeneous environment, spatial variation in vital rates can also be important[11]. To make matters worse, spatial and temporal variation in the distribution of vital rates could interact. Because we do not know how important spatial and temporal variation in life-history rates are, a useful exercise would be to look for systematic variation in the distributions of population growth rates and vital rates across species and populations using data from long-term studies.

By only selecting long-term studies, Brook *et al.* meet this first criterion. However, many conservation managers do not have the luxury of such data but they still use PVAs that might produce unreliable predictions on which flawed conservation strategies are based.

Criterion two: future distributions

The second criterion is that if good estimates of the distribution of vital rates can be made, are the shapes, means, temporal variances and autocorrelation of these distributions likely to apply into the future? Usually, it is impossible to know the answer to this in most cases. There are biotic and abiotic phenomena that can lead to changes in the shape, mean, temporal variance and autocorrelation of these distributions over time[11–13]. Such processes can be classified into two categories: (1) those that are the result of a catastrophe[5]; and (2) those that result in a longer-term change in the processes and vital rates that limit the population growth rate[12]. In the examples that Brook *et al.* use, there appears to have been constant dynamics over at least ten years. However, their sample cannot be assumed to represent all cases and, in principle, it seems probable that small and endangered populations are more likely to show changed dynamics over time as a result of either environmental, anthropogenic or intrinsic processes than are large and unendangered populations.

Catastrophic events rapidly decrease the size of a population and could have precipitated the majority of extinctions[14]. The frequency distribution and consequence of such events is rarely known[15]; consequently, parameterizing a population model to include the probability of a catastrophe occurring in a specified time period is little more than guesswork. There are exceptions; for example, the distribution of catastrophic fires can be estimated from palaeontological data[16]. Even in cases when the distribution of catastrophes is unknown, it is sensible to model the potential impact of catastrophes of known effect, to devise management or conservation strategies that could cope with such eventualities[3].

Many processes can lead to a change in the key vital rates and factors limiting the growth rate of a population. For example, a population released from predation, possibly by the local extinction of a predator, could increase at a rate limited only by the maximum reproductive potential of each adult female but, once the population approaches carrying capacity, density-dependent processes will begin to limit the population through resource availability. Such a shift in the dynamics does more than affect the distribution of vital rates. The change from predator limitation, through limitation by reproductive potential, to limitation by resource availability, shifts the key vital rate from juvenile survival, to the birth rate, to adult survival[12,13]. Many processes can have profound effects that lead to changes in the factors regulating a population and the distribution of vital rates. For example, changes in the habitat resulting from succession, anthropogenic land use or some habitat-modifying catastrophes, changes in the structure of the community resulting from species colonization or extinction, the introduction of noncatastrophic diseases, changes in hunting pressure and changes in the weather as a result of global climate change. Many PVA models allow changes in habitat to be incorporated through clumsy mechanisms, such as increasing K deterministically. Considerably more work needs to be done to allow more sophisticated habitat dynamics to be included in models, as has been attempted in the metapopulation modelling program ALEX (Analysis of the Likelihood of Extinction) (Ref. 17).

Conclusions

So how and when should PVAs be used? We conclude that predictions of future population sizes and quasi-extinction events can only be accurate if managers are confident that their data adequately capture the distribution of population growth rates and/or vital rates. If their data are poor, the predictions of PVAs should be treated with extreme caution and possibly even ignored entirely.

Predictions will only be useful if it is known that the distributions of the population growth rate and vital rates will not change in the future. As ecological systems are dynamic, regulating processes can change, but it is usually impossible to predict how or when. Research is required to estimate how changes from one regulating factor to another influence the distribution of vital rates and population growth rates. In such cases, PVA models could be developed to be adaptive. Data on the population growth rate and/or vital rates should be collected following the initiation of a management or conservation strategy, and the results and predictions of PVAs should be reassessed, and if necessary strategies altered, following the addition of these data. In our view, PVAs could be useful for comparing the consequences of different management or conservation strategies, and for exploring theoretically the implication of model assumptions on extinction probabilities and population dynamics[18]. However, we doubt the general claim that they can be accurate in their ability to predict the future status of wild populations.

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